SYSTEMATICS AND BIOGEOGRAPHY OF EASTERN AUSTRALIAN CHAROPIDAE (MOLLUSCA, PULMONATA) FROM SUBTROPICAL RAINFORESTS

JOHN STANISIC

Stanisic, J. 1990 12 24: Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. *Memoirs of the Queensland Museum*, 30(1):1–241. Brisbane. ISSN 0079-8835.

Fifty land snail species in 18 genera of Charopidae from eastern coastal Australia are reviewed. *Ngairea*, *Lenwebbia*, *Omphaloropa*, *Nautiliropa*, *Coenocharopa*, *Biomphalopa* and *Rotacharopa* are new. *Egilodonta* Iredale, 1937 is placed in synonymy with *Rhophodon* Hedley, 1924. *Ngairea levicostata*, *N. canaliculata*, *Mussonula fallax*, *Hedleyoconcha ailaketoae*, *Lenwebbia protoscrobiculata*, *Setomedea monteithi*, *S. nudicostata*, *S. janae*, *Gyrocochlea paucilamellata*, *Rhophodon minutissimus*, *R. colmani*, *R. elizabethae*, *R. kempseyensis*, *Cralopa carlessi*, *C. kaputarensis*, *Egilomen globosa*, *Elsothera genithecata*, *Omphaloropa varicosa*, *Coenocharopa sordidus*, *C. macromphala*, *C. yessabahensis*, *C. parvicostata*, *C. multiradiata*, *C. alata*, *Rotacharopa annabelli*, *R. kessneri*, *R. densilamellata* (27 species) are new. Neotypes are nominated for *Helix murphyi* Cox, 1864, *Helix omicron* Pfeiffer, 1851 and *Rhophodon peregrinus* Hedley, 1924. All except 3 species are assigned to the Charopinae; those 3 species, assigned to the Rotadiscinae, are the first record of the subfamily in Australia.

Analysis of shell and anatomical patterns is presented: differences in shell, radular, pallial and genital structures are evaluated. Patterns of variation are correlated with three levels of functional and ecological significance - species recognition, exploitation of adaptative zones, and the need to conserve water. Morphological patterns of Australian species are compared with those of New Zealand and the Pacific Islands and their relationships are discussed.

The proposed phylogeny identifies major morphological trends and multiple origins of the fauna. A cladistic analysis (PAUP) utilises 75 shell and anatomical characters. A biogeographic synthesis integrates distributions, ranges, and ecology with aspects of past climatic, geologic and vegetational change. Charopid evolution in eastern Australia is closely linked to climate induced changes in mesic communities since the Cretaceous.

☐ *Mollusca, Pulmonata, Charopidae, Systematics, Phylogeny, Biogeography.*

John Stanisic, Queensland Museum, PO Box 300, South Brisbane, Queensland 4101, Australia; 19 October 1989.

The Charopidae is a family of small to minute, radially ribbed, pulmonate land snails abundant in leaf litter of eastern Australian rainforests. A few species also occur in drier forests throughout the rest of the continent. Burch (1976), based on the earlier checklists of Iredale (1937a, 1937b, 1941a, 1941b), listed 110 species and 29 genera of Charopidae from Australia.

The Australian Museum/Queensland Museum east coast rainforest surveys of the mid-1970's recorded 38 charopid species (28 new) from northern New South Wales, southern and central Queensland (Broadbent and Clark, 1976). Surveys by the Queensland and Australian Museums (1981-1983) in subtropical rainforests of northern New South Wales and southern Queensland revealed an even greater number of undescribed species from this region. Collecting by the author has exposed extensive radiations of charopids in central Queensland mesic forests and on the mountain peaks of the Ingham-Cooktown rainforest massif in tropical Queensland (Stanisic, 1987). Previously, the Charopidae were regarded as a mainly cool temperate group with greatest diversity in Victorian and Tasmanian forests.

In general, eastern Australian charopids display an intimate ecological bond with rainforests.

Most of the 50 species (18 genera) reviewed have subtropical distributions although it has been necessary to include several temperate and tropical taxa. The aims are to initiate a survey of the subtropical Charopidae, to identify patterns of conchological and anatomical variation, and to place them in biogeographical context. The species reviewed here may represent only 15% of Australian charopids. Therefore phylogenetic conclusions are based on the analysis of a seemingly mosaic pattern of variations.

Subtropical eastern Australia is defined as the coastal to subcoastal area between Dorrigo, New South Wales and Rockhampton, Queensland. Floristically, this area encompasses the distribution of dry and moist subtropical closed forests (Fig. 1).

ABBREVIATIONS USED

Institutions

AM	Australian Museum, Sydney
BMNH	British Museum (Natural History), London
FMNH	Field Museum of Natural History, Chicago
NMV	Museum of Victoria, Melbourne
SAM	South Australian Museum, Adelaide
QM	Queensland Museum, Brisbane

Collectors/Collection Data

AM/QM-ABRS: Australian Biological Resources Survey funded field work (1981–1983) involving various collectors from the Australian and Queensland Museum.

Earthwatch/QM: American Earthwatch sponsored fieldwork involving volunteers and various staff of the Queensland Museum.

Vegetation Types

CNVF, complex notophyll vine forest; NVF, notophyll vine forest; MVF, microphyll vine forest; CMVF, complex mesophyll vine forest; SEVT, semi-evergreen vine thicket; SMVFF, simple microphyll vine fern forest; SMVFT, simple microphyll vine fern thicket.

Anatomical Terminology

DG, prostate; E, epiphallus; EC, epiphallic caecum; EF, epiphallic flagellum; EP, epiphallic pore; EPP, epiphallic pilaster; ERC, epiphallic retractor caecum; G, ovotestis; GD, hermaphroditic duct; GG, albumen gland; GT, talon; H, heart; HG, hindgut; HV, principal pulmonary vein; I, intestine; K, kidney; KD, ureter; KX, ureteric pore; MA, mantle lobe; MC, mantle collar; MG, mantle gland; P, penis, PP, penial pilaster; PPM, main penial pilaster; PPT, preputial tube; PRM, penial retractor muscle; PV, penial verge; S, spermatheca; SP, spermatophore; SS, spermathecal stalk; UT, uterus, UV free oviduct; UVP, free oviduct pilaster; V, vagina; VC, vaginal caecum; VD, vas deferens; X, carrefour; Y, atrium; Z, digestive gland.

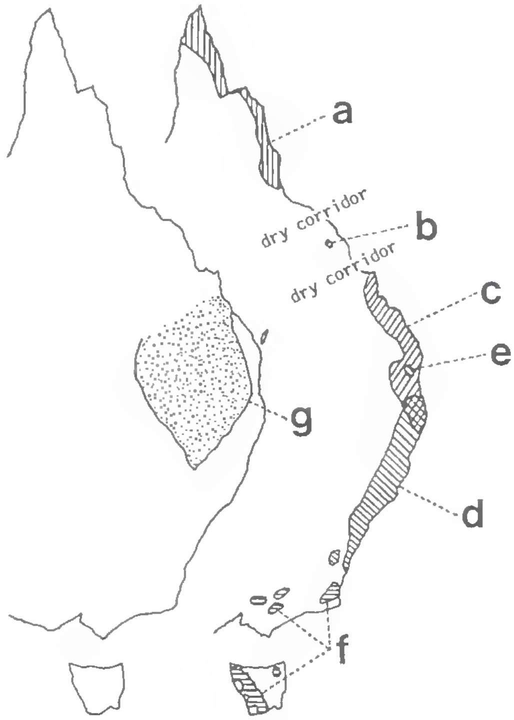


FIG. 1. Distribution of selected rainforest floristic regions, provinces and areas in eastern Australia. a, humid tropical northern region; b, subtropial forests of the Eungella area; c, dry to moist subtropical province; d, warm temperate to cool temperate province; e, temperate forests of the Lamington Plateau; f, cool temperate province; g, dry subtropical province. (Adapted from Webb and Tracey, 1981).

MATERIAL

This study is based on 6230 specimens mainly in the Queensland Museum, Brisbane and the Australian Museum, Sydney. Most specimens have been collected since 1980. 'Wet' material available was <10% of the total specimens; 150 specimens (44 species) were dissected.

The material contains a high proportion of juvenile and subadult specimens because in the early stages, when species presence was being established, most specimens were obtained by extraction from collected litter. This material consisted of a large number of dead juveniles which reflects the overall higher field mortality among young snails. Later collecting was concentrated on live adults for dissection; so 'wet'

FIG. 2. Distribution of major rainforest areas in northern New South Wales and southern Queensland.

material includes a greater proportion of adults. However, because many species are difficult to locate live in the field, individual 'wet' lots often contain only single or few specimens.

Seasonal climatic effects may be a contributing factor to the numbers of live adults versus live subadults present at any time, but the small amount of wet material and uneveness of collecting effort through the year prevent sensible conclusions; only a few species were abundant enough for seasonal studies.

Line drawings of shells and dissections were made by the author using a camera lucida attachment.

Measurements are recorded using the method of Solem (1976, pp. 11–15).

PREVIOUS STUDIES

Previous studies of Australian Charopidae have been introductions in broader faunal checklists except for works of Hedley (1924), Solem (1984), Smith and Kershaw (1985) and Stanisic (1987) who dealt specifically with Australian charopids. With the exception of Hedley (1889), who figured the radula and jaw of *Hedleyoconcha delta* (Pfeiffer, 1857), and Odhner (1917) who figured the jaw and radula of *Pilsbrycharopa tumidus* (Odhner, 1917), malacologists of the late 19th and early 20th century used conchological details to establish species and genera. Smith and Kershaw (1985) and Stanisic (1987) provided anatomical details for several genera and species from the Tasmania-Victoria and north Queensland areas, respectively.

Iredale (1937a, 1937b) compiled records up to that date. Subsequent works introducing new species are Gabriel (1947), Gabriel and Macpherson (1947), Cotton (1939), Iredale (1937c, 1939, 1941) and Stanisic (1987).

Most early shell-based descriptions are of little value in contemporary systematics. Only Hedley (1912, 1924) set an acceptable standard. Solem (1983) set a modern standard with his review of Pacific Island taxa; he showed the importance of soft parts in species diagnoses.

CLASSIFICATION

Solem (1983, p. 47) presented a full synonymy of the family level units available for the endodontoid complex, and in the Charopidae included Flammulinidae Crosse, 1894, Dipnelicidae Iredale, 1937 and Hedleyoconchidae Iredale, 1942. These family names had previously been applied to various subdivisions of the Australian Charopidae by Gabriel (1930) and Iredale (1937a, 1941b, 1942). Solem (1983, p. 70) recognised five subfamilies: Otoconchinae Cockerell, 1893, Rotadiscinae Baker, 1927, Charopinae Hutton, 1884, Semperodoninae Solem, 1983, and Trukcharopinae Solem, 1983. The Charopinae was broadly defined and considered amenable to subdivision subsequent to a revision of Australian and New Zealand taxa.

The phylogeny developed in this study utilises anatomical features to define subfamilial, generic and species units. Specifically, the structure of the pallial cavity, gross morphology of the reproductive system, and internal characteristics of the terminal genitalia are considered important criteria for phylogeny. Conchological detail such as shell shape, ribbing, and coiling pattern may be convergent and often mask quite crucial differences in anatomy. However, some conchological features including apical sculpture, microsculpture and primary shell sculpture show more positive correlations with underlying anatomical patterns. Hence it has been possible to produce a practical classificatory system which utilises shell features. Because this introductory study investigates selected species from an area of mid-range diversity for the family, phylogenetic gaps between genera are not 'even'; they reflect the diverse ecological habits of species studied.

Genera reviewed and, where possible, redefined using both shell and anatomical features are:- *Cralopa, Discocharopa, Elsothera, Gyrocochlea, Mussonula, Rhophodon, Setomedea, Hedleyoconcha, Egilomen, Letomola.*

Egilodonta is synonymised with *Rhophodon.*

DISTRIBUTION, HABITAT, ECOLOGY AND CONSERVATION

In eastern Australia, charopids are mainly found in closed forests (= rainforests). Historical development of this association is examined further in the biogeographic discussion. The strength of this association, antiquity of the Charopidae, and long-term historical persistence of mesic forests in eastern Australia, have combined to produce a complex pattern of narrow, wide, disjunct and relict distributions.

During arid phases of the mid to late Tertiary, rainforests would have acted both as refugia and epicentres of charopid evolution. Today all Australian rainforests are refugia (Webb and Tracey, 1981).

Charopids flourish in the four major categories of rainforest refugia of Webb and Tracey (1981):- A, large, relatively wet areas such as the Border Ranges of southern Queensland, the Dorrigo Plateau, NSW, and mountain summits such as Mt Warning, NSW, and Mt Glorious, SEQ; B, small, relatively dry, topographic isolates which include rocky limestone outcrops such as the Caves, near Rockhampton, MEQ, Mt Biggenden, SEQ, and the Kempsey Caves complex, NSW - besides providing protection from fire and a relatively high level of moisture, these areas also offer an abundant supply of calcium; C, small edaphic isolates where soil types are critical in determining rainforest existence - gallery forests growing on riverine alluvia and the deciduous forests of Cooloola, SEQ, are examples; D, mountain tops in lower rainfall areas where topography, soils and climate combine to ensure persistence of closed forests - examples are the Bunya Mountains and areas of the Many Peaks Range, SEQ and Mt Dryander, MEQ. In NQ and MEQ charopids are mainly restricted to montane regions indicating that past environmental changes have been effective in geographically cornering of species. This altitudinal factor is less noticeable in the subtropical region where both lowland and foothill rainforests have a rich complement of species.

Although rainforest provides ample litter containing a variety of living spaces through which snails can crawl, species investigated here do not exploit the litter zone. *Hedleyoconcha* is arboreal with *H. delta* living on the leaves of trees and shrubs. *Ngairea* and *Sinployea* are semiarboreal preferring to live under the bark of fallen, rotting trees. *Lenwebbia* has been found sitting in the open on rotting logs while *Setomedea* is the only group known to prefer very damp places in or under logs. Living under logs is the preferred habit for *Nautiliropa, Gyrocochlea, Biomphalopa, Elsothera, Rotacharopa, Cralopa stroudensis, C. kaputarensis,* and *Egilomen globosa.* Species of *Rhophodon, Letomola contortus* and *Coenocharopa yessabahensis,* live on rock surfaces and some (e.g. *C. yessabahensis*) show habitat-related radular specialisation. *Coenocharopa alata* lives in moss on logs and rocks, while *C. macromphala* and *C. sordidus* probably live among the friable earth below the litter, as do *Omphaloropa varicosa* and *Egilomen cochlidium.* Microhabitats of the other species are unknown.

Feeding habits are unknown. Radular morphology is conservative; rarely (e.g. in *Nautiliropa omicron* and *Ngairea corticicola*) is there any structural indication of possible dietary shift.

Sympatry has been noted in *Rhophodon, Ngairea, Gyrocochlea* and *Coenocharopa.* Microsympatry has been observed between *Ngairea dorrigoensis* and *Ngairea corticicola* with the two species having been collected from under the same piece of bark. These examples are discussed in more detail in the systematic review under the relevant taxonomic heading.

Species are largely restricted to rainforest and in some instances e.g. *Rhophodon elizabethae* and *Setomedea nudicostata*, are confined to very small patches. In many cases, particularly in northern NSW and southern Queensland, clearing for agriculture and other human activity has drastically reduced lowland and upland rainforest. Whether or not species will survive this synanthropic fragmentation of habitat remains to be seen.

Charopids are useful indicator species of bush quality. Areas where diversity is high, or where restricted species reside have special refugial significance.

TABLE 1. Mean shell measurements in 49 species of east Australian Charopidae

	MINIMUM	FIRST QUARTILE	MEDIAN	THIRD QUARTILE	MAXIMUM
WHORL COUNT	3 1/2-	4 1/8	4 1/2-	4 3/4-	6 1/8+
SHELL HEIGHT (MM)	0.49	1.14	1.71	2.94	6.01
H/D RATIO	0.40	0.52	0.56	0.60	0.81
SHELL DIAMETER (MM)	1.12	2.15	3.08	5.35	7.91
D/U RATIO	2.32	2.68	3.58	8.15	closed
RIBS ON BODY WHORL[1]	26.8	59.1	80.0	118.3	279.7
RIBS/MM[1]	1.96	5.56	7.24	11.26	33.34
BODY WHORL WIDTH (MM)	0.23	0.72	0.99	1.79	3.50

[1] Fourteen species with reduced and irregular ribbing were omitted from these figures.

PATTERNS OF VARIATION

SHELL

Size and shape – Whorl count (Table 1) is usually (33 species) 4-5; four species have <4 whorls while 12 species have 5 or more whorls. Higher whorl numbers occur in several different lineages. *Hedleyoconcha delta* has the largest number of whorls with 6 1/8+ average; *Rotacharopa annabelli* has 5 3/4- whorl average (Figs 23a, 140a); *Biomphalopa recava* and *Setomedea monteithi* have mean whorl counts of 5 1/4-; *Ngairea murphyi* has mean of 5 1/2-.

Discocharopa aperta with 3 1/2- whorls has the lowest whort count (Fig. 93a), while *Sinployea intensa* with 3 5/8+ whorl average (Fig. 137a), is near the minimum mean whorl count for Pacific Basin *Sinployea* (Solem, 1983, p. 83). The highly modified *Letomola contortus* (Fig. 67a–c) has a mean whorl count of 3 7/8-.

Species with low whorl counts tend to be small in size, but the opposite does not apply to species with high whorl counts. Of those species with average whorl count >5, six are <3 mm in diameter. Only *Hedleyoconcha delta*, *H. ailaketoae*, and *Ngairea murphyi* have mean diameters which fall into the upper quartile range. Significantly these three species have strongly keeled body whorls. Hence whorl addition does not appear to have been a major factor in attaining large size.

The largest species is *Gyrocochlea vinitincta* while *Discocharopa aperta* is the smallest. Between these extremes of shell diameter a significant number of species fall into the 1st to 2nd quartile range which covers about 27% of the total range of variation (Table 1). In contrast, the larger species show a much greater size range, suggesting that repeated evolutionary experiments in size increase occurred. This conclusion is further supported by the many different shell morphotypes represented among larger species.

Nine of the 15 largest species belong to genera which have an incomplete secondary ureter and elevated, keeled shells. Only *Lenwebbia protoscrobiculata*, and *Setomedea*, which show several secondary conchological and anatomical specialisations, have incomplete secondary ureters and more average-sized shells. Other large species belong to *Gyrocochlea*, *Nautiliropa*, and *Elsothera*.

Conservatism in H/D ratios (Table 1) emphasises stability of shell shape. Prominently high spired species, *Ngairea levicostata* (Fig. 6c), *Mussonula verax* (Fig. 18c), *Hedleyoconcha delta* (Fig. 23c) and *H. ailaketoae* (Fig. 6e) have an above average H/D ratio that is >0.70. High H/D ratio in *Egilomen globosa* is due to greater spire protrusion, closed umbilicus and sharp deflection of the body whorl (Figs 131a-c), whereas high whorl count, narrow umbilicus and more protruded spire produce an above average H/D ratio in *Rotacharopa densilamellata* (Figs 146a-c). In *Ngairea* and *Mussonula*, spire protrusion and large body whorl width contribute to increased height of shell, while in

Hedleyoconcha delta, above average whorl count is a further mitigating factor. In contrast the height of *Gyrocochlea*, which has a strongly depressed spire, is due to a combination of large body whorl and dramatic deflection of the body whorl in the last third of its volution.

Umbilical width varies from closed in some species of *Cralopa* and *Elsothera* (Figs 101b, 104b, 106b, 108b) to widely open in *Omphaloropa*, *Discocharopa* and *Rhophodon* (Figs 71b, 74b, 77b, 78b, 81b, 84b, 87b, 93b). An open umbilicus is most common; a narrow umbilicus occurs mainly in groups with altered whorl contour. *Hedleyoconcha*, *Mussonula* and *Ngairea* (except *N. murphyi*) have very small umbilici and angulate to keeled body whorls. *N. murphyi* has secondarily narrowed whorls and more open umbilicus (Fig. 9b). In *Egilomen globosa* (Fig. 131a,b), *Rotacharopa densilamellata* (Fig. 146a,b), *R. kessneri* (Fig. 143a,b), and *R. annabelli* (Fig. 140a,b) with tightly coiled shells, whorls are globose and expanded, constricting the umbilicus with their inner margins. Umbilical contour varies from narrow U-shaped, through wider V-shaped to wide saucer-shaped in *Rhophodon kempseyensis* (Fig. 78b) and *Discocharopa aperta* (Fig. 93b).

Whorl profiles range from laterally compressed in *Coenocharopa alata* and *Rhophodon bairnsdalensis* (Figs 117c, 89c) to strongly keeled in *Ngairea murphyi* and *Hedleyoconcha delta*. In *Letomola contortus* whorl profile is altered by a supraperipheral sulcus (Fig. 67c). A weak supraperipheral sulcus is also present in *Elsothera nautilodea* (Fig. 106c), and *Coenocharopa macromphala* (Fig. 114c).

Sutures are generally weakly impressed although *Cralopa stroudensis* has a very deep suture (Fig. 95a), and *Gyrocochlea vinitincta* (Fig. 45a) and its congeners initially have a weakly impressed suture which becomes deeply furrowed as the last whorl descends. A more unusual development in *Ngairea canaliculata* and *Elsothera genithecata* is a narrow channel at the sutural area (Fig. 12a). Apertural sinuses are developed in *Cralopa* and *Elsothera*.

Sculpture - Spiral apical sculpture is prominent in *Sinployea intensa*, *Omphaloropa varicosa*, *Setomedea* and *Mussonula*. *S. intensa* has low broad spiral cords (Fig. 137d) while *O. varicosa* has the cords narrower and slightly higher (Fig. 134e). In *Setomedea seticostata* and *S. janae* they are regularly spaced and similar to those of *O. varicosa*, whereas in *S. monteithi* (Fig. 41e), *S. nudicostata* (Fig. 35e), and *Setomedea* sp. (Fig. 44e), the cords become squiggly, and vague curved radial ridges develop at the nuclear-postnuclear boundary. Radial elements on the latter part of the protoconch are more pronounced in *Mussonula verax* Iredale, 1937 (Fig. 18d) and *M. fallax* (Fig. 20f). In *Gyrocochlea paucilamellata* apical sculpture is finely reticulate with spiral and radial elements equally prominent (Fig. 51e) whereas in *G. vinitincta* (Fig. 45e) and *G. convoluta* (Fig. 48e) the radials are low weak ridges which are raised at their intersection with the spiral cords to form tiny beads. In contrast, *G. curtisiana* (Fig. 64a) has apical sculpture which initially is a series of regularly arranged "pits" then becoming irregularly, radially ribbed toward the end of the protoconch. *Biomphalopa recava* (Fig. 57e), *B. concinna* (Fig. 60e) and *Nautiliropa omicron* (Fig. 63d) have similar apical pitting. A different pattern of apical pits in *Hedleyoconcha delta* has deeper and more crowded depressions (Fig. 23e). Even in this case, the vague radial pattern of pits indicates probable derivation from a typical reticulate pattern. *Lenwebbia protoscrobiculata* has a similar but finer pattern (Fig. 29g). In *Ngairea murphyi* irregular radial wrinkles and shallow irregularly shaped pits combine (Fig. 9f); apparently a modification of radial ribs and spiral grooves seen in *N. corticicola* (Cox, 1866) and *N. levicostata* (Figs 6d, 15e). *Letomola contortus*, has apical sculpture like that of *N. murphyi* but with an underlying radial pattern which is less conspicuous, producing a malleate surface (Fig. 67d).

Spiral grooves on the protoconch are rare occurring in *Ngairea corticicola* (Fig. 15e), *N. canaliculata* (Fig. 12f), and to a lesser extent *N. levicostata* (Fig. 6d). *N. dorrigoensis* has predominantly radial apical sculpture with very fine spiral lines visible in the sutural area (Fig. 3d).

Apical sculpture most commonly consists of prominent radial ribs and less prominent spiral cords. Radials may be crowded (*Elsothera*, *Cralopa*, *Discocharopa*), widely spaced (*Egilomen*) or widely spaced initially, becoming more crowded toward the nuclear-postnuclear junction (*Rhophodon*, *Coenocharopa*). Spirals may be continuous, narrow, squiggly cords (*Cralopa*, *Elsothera*, *Coenocharopa*), short, wrinkle-like cordlets (*Rhophodon*, *Discocharopa*), or inconspicuous (*Egilomen*). If the cords are continuous they are usually visible on the apices of the radial ribs.

Apical sculpture of *Rotacharopa* appears reticulate under the light microscope, but highly complex under the SEM. The radials are a series of curved ridges which become broader toward the nuclear-postnuclear sculpture (Fig. 146d). Spirals, while appearing continuous, are a series of short segments (Figs 140e, 146c). This apical sculpture was also reported in *Microcharopa mimula* Solem (1983, p. 70).

Postnuclear sculpture involves variations on the pattern of major radial ribs and microsculpture of microradials and low spiral cords. Major departures are seen in species with an incomplete secondary ureter. Periostracal enhancements may be present and take the form of high blades on the major radials as seen in *Nautiliropa omicron* (Fig. 63e) or the expanded peripheral extensions of *Coenocharopa alata* (Fig. 117e,h). A more significant change takes place in *Setomedea* which has periostracal setae along the length of the major ribs (Figs 32f, 38f, 41f).

Major radial ribs may be broad and high as in *Biomphalopa recava* (Fig. 57f), *Gyrocochlea vinitincta* (Fig. 45f), *Egilomen cochlidium* (Fig. 128g) and *Rhophodon peregrinus* (Fig. 71f), have a high periostracal blade as in *Nautiliropa omicron*, *Omphaloropa varicosa*, and *Rotacharopa* (Figs 63e, 134f, 140f), or be reduced with a low periostracal blade expanded at the shell periphery as in *Coenocharopa alata* (Fig. 117g), and *C. parvicostata* (Fig. 120d). In *Mussonula verax* (Fig. 18e), *M. fallax* (Fig. 20g), and *Ngairea levicostata* (Fig. 6e), the periostracal blade is high and continuous above a low radial rib. However, the blade is not vertical as in *O. varicosa*, but instead is folded back toward the shell apex. In *Setomedea* the major ribs have two periostracal blades (Figs 32f, 38f). Rib height reduction is seen in *Lenwebbia protoscrobiculata* which has very low radial undulations on adult whorls (Fig. 29f), *Ngairea corticicola* which has widely spaced low, radial undulations with a deciduous periostracal blade (Fig. 15f), *Letomola contortus* which has an overlapping shingle-like arrangement of radial thickenings (Fig. 67e), and *Coenocharopa yessabahensis* which has very low, crowded radial ribs (Fig. 123g). *Ngairea murphyi* (Fig. 9g), *N. dorrigoensis* (Fig. 3e), *Hedleyoconcha delta* (Fig. 23f) and *H. ailaketoae* (Fig. 26d) have crowded, reduced, and thread-like major ribs to the exclusion of microradials.

Most species have regular radial ribbing. An average pattern is shown by *Biomphalopa recava* (Fig. 57a) and *Setomedea seticostata* (Fig. 32d). Reduction and increase in rib counts occur in both small and large species of several genera. Widely spaced ribs of *Rhophodon bairnsdalensis* (Fig. 89a), *Egilomen cochlidium* (Figs 128a,e) and *Gyrocochlea paucilamellata* (Fig. 51a), crowded ribs of *Biomphalopa concinna* (Fig. 60a,d), *Rhophodon minutissimus* (Fig. 84a), and *Rotacharopa kessneri* (Fig. 143a), *Gyrocochlea curtisiana* (Fig. 54a), *Elsothera nautilodea* (Fig. 106a) and *Rotacharopa densilamellata* (Fig. 146a), and the exceptional situation in *Rhophodon kempseyensis* which has a rib count of 279.7 (Fig. 77a), are examples of the variation encountered. Species of *Coenocharopa* (with the exception of *C. yessabahensis*) have reduced rib counts. However, the deciduous, periostracal nature of the ribs, combined with the worn state of most of the available material, made rib counts in these species difficult.

Reduction in primary radial sculpture may therefore involve reduction in rib counts through increased rib spacing, as well as a reduction in the height of the major ribs.

Microsculpture typically consists of high crowded radial riblets and low, narrow crowded spiral cords buttressing the radials on either side e.g. *Elsothera sericatula* (Fig. 104f), *Gyrocochlea vinitincta* (Fig. 45f), *Biomphalopa concinna* (Fig. 60f) and *Cralopa stroudensis* (Fig. 95e). *Rhophodon* and *Rotacharopa* have high microradials but very low broad spiral cords with small elongate beads formed at their intersection (Figs 71f, 89e, 143f, 146f); *Rhophodon kempseyensis* (Fig. 77e), and *Discocharopa aperta* (Fig. 93f) have the microradials divided into a series of short segments; *Sinployea intensa* (Iredale, 1941) has the microradials more thread-like and spiral cords conspicuous with elongate beads at the intersections (Fig. 137e); and *Egilomen cochlidium* (Fig. 128g) and *E. globosa* (Fig. 131f), have spirals more conspicuous than microradials. This latter condition is taken a step further in *Omphaloropa varicosa* where microradials are very low and microspirals form large beads at the intersection such that interstitial areas appear to be sculptured with spirally arranged beads (Fig. 134f). Reduction in the height of microradials also occurs in *Coenocharopa*. However, the microradial element attains height by the addition of fine thread-like periostracal blades e.g. *C. alata* (Fig. 117g). Microradials may be higher, equal in height or lower than the microspiral cords, but there are no beads formed and there is no buttressing.

More complex departures from the above patterns of microsculpture are seen in species with an incomplete secondary ureter. *Setomedea* has conspicuous microradials which are higher than the thread-like microspirals, and although the microspirals continue up the sides of the microradials there is no buttressing (Figs 32f, 35f). *S. janae* has microradials with a scalloped profile (Fig. 38g) as a result of the microsculpture dipping into spiral furrows in the shell surface. These undulations are also developed in *S. monteithi* and *Setomedea* sp. *Lenwebbia protoscrobiculata* has only microspiral grooves on the early part of adult whorls, but a combination of fine thread-like microradials and grooves on the latter part of the body whorl (Fig. 29e,f). Spiral grooves are present on shells of *Ngairea corticicola* (Fig. 15f) and *N. canaliculata* (Fig. 12g). On the other hand *N. levicostata* has microsculpture of fine spiral lines (Fig. 6c) simliar to *Mussonula fallax* (Fig. 20g). *M. verax* appears to lack the fine spiral lines of *M. fallax*, but this needs to be confirmed. *Ngairea dorrigoensis* (Fig. 3c) and *N. murphyi* (Fig. 9a,e) lack microradials, but have many crowded, low, thread-like radials crossed by crowded thread-like microspirals. Low reticulate sculpture also occurs in *Hedleyoconcha delta* (Fig. 23f) and *H. ailaketoae* (Fig. 26d), where spiral cords and radials are fused. *Hedleyoconcha* exhibits an unusual growth-related change in sculpture; after about 4 1/2 whorls the reticulate pattern is replaced by a much less sculptured pattern of irregularly spaced radial growth ridges (Figs 23a, 26a).

Apertural Barriers - Apertural barriers were recorded in *Letomola contortus* and *Rhophodon*. However, barrier formation is even more widespread among east-coast subtropical charopids. Several undescribed taxa with barriers live between Gympie and Rockhampton; until these are described, discussions on barrier formation will remain, skeletal.

The form and surface characteristics of barriers in *Letomola contortus* separate them from those in *Rhophodon*. Without exception *Rhophodon* spp. have numerous parietal and palatal barriers whose overall effect is to reduce the apertural area. In contrast *L. contortus* has only a single, thin blade-like parietal barrier (Fig. 68a), no barriers on the outer lip margin, and a low ridge-like basal palatal (Fig. 68b). Furthermore, the barrier surface in *L. contortus* has small rounded protrusions (Fig. 68c) whereas *Rhophodon* has narrow to broad transverse ridges angling up from the barrier surface (Figs 78c, 81d, 84d). *R. kempseyensis* (Fig. 78c), and *R. minutissimus* (Fig. 84d), display extremes of variation. These basic differences indicate separate derivation of the barriers in the two genera.

In *Rhophodon* the number, size and shape of barriers as well as surface sculpture are variable. Generally the parietal barriers are more blade-like in form than the shorter crescent-shaped palatal barriers. The number of parietal barriers is least in *R. bairnsdalensis* which has a single elongate barrier (Fig. 90a), and ranges to the four barriers and two traces present in *R. peregrinus* (Fig. 71g). Typically there are three blade-like parietals - a horizontal lamella about halfway down the whorl margin, and two on the lower part of the parietal wall, deflected downwards. *R. elizabethae* has only two parietal lamellae but has a well-developed, low, blade-like superior parietal trace. In *R. peregrinus* the first parietal is deflected upwards while the second, third and fourth are directed downwards (Fig. 71g). An accessory parietal trace is also present in *R. consobrinus* (Fig. 74h). Usually the parietal barriers have a long anterior taper projecting beyond the edge of the aperture and an expanded posterior section with an abruptly tapered resorption edge. *R. peregrinus* has recessed parietals which have shortened or no anterior tapers (Fig. 71g). A similar shortening is seen in the deeply recessed second parietal of *R. minutissimus* (Fig. 84g). The only other notable variation is in *R. colmani* which has the parietals greatly swollen, particularly at the posterior edge, thus further reducing the apertural opening (Fig. 87f).

Columellar barriers range from well developed, horizontal lamellae in *R. elizabethae* and *R. colmani* (Fig. 87h) to fine, almost thread-like in *R. peregrinus* and *R. consobrinus*.

Palatal barriers vary from two in *R. bairnsdalensis* (Fig. 90b,c) to six in *R. colmani* (Fig. 87g). A superior palatal trace, situated very near to the palato-parietal margin, may also be present. The first palatal barrier is usually situated at the baso-columellar margin and is a short, high, crescent-shaped lamella. The shape in *R. colmani* is typical. Remaining palatal barriers are similar in shape though somewhat reduced in height. In *R. peregrinus* the upper palatals have a slightly elongate anterior taper (Fig. 71h), while those in *R. colmani* have the anterior edge much more markedly tapered. The low thread-like upper palatal of *R. bairnsdalensis* (Fig. 90c) is a further variation.

ANATOMY

44 of 50 species were dissected. Species not dissected are *Mussonula verax*, *Hedleyoconcha addita*, *Rhophodon colmani*, *Discocharopa aperta*, *Elsothera nautilodea*, and *Coenocharopa multiradiata*. Available material of *Mussonula fallax* and *Ngairea levicostata* had immature reproductive systems which provided no details on genital structures. Poor preservation led to obtaining only fragmentary detail of the penis interior of *Sinployea intensa* and pallial cavity of *Coenocharopa parvicostata*.

Variations in the pallial and genital anatomy are minor and reflect regional endemicity. With the exception of *Rotacharopa* and the predominantly southern *Elsothera* the patterns are conservative.

Pallial Cavity - Typically the pallial cavity has a well-developed mantle collar with mantle gland extending onto the pallial roof, a weakly bilobed kidney in which the pericardial lobe is vaguely triangular and much longer than the rectal lobe, and a complete secondary ureter with the ureteric pore situated at the inner edge of the mantle collar adjacent to the anus. The hindvein is conspicuous, but lacks prominent branching.

A major departure from this pattern occurs in *Ngairea*, *Hedleyoconcha*, *Lenwebbia*, *Mussonula*, and *Setomedea* which have an incomplete secondary ureter that is a very short reflexed tube with the ureteric pore situated at the rear of the pallial cavity in the angle between the kidney and the hindgut (Figs 7, 10e, 21, 24g, 30e, 33g). Whether or not these taxa should be given separate subfamilial recognition is uncertain and will remain so until more of the southern taxa are dissected.

In most species the primary ureter is a simple tube running from the kidney apex to the rear of the pallial cavity. However, some taxa with an incomplete secondary ureter have undergone elongation of the primary ureter. This is most obvious in *Setomedea* which has the initial part of the primary ureter coiled (Figs 33g, 36e, 39f, 42f), and in *Lenwebbia* which has it conspicuously reflexed (Fig. 30e). Less noticeable are the subtle variations seen in *Ngairea* and *Mussonula* (Figs 4e, 13e, 16f, 21) where some degree of reflexion also occurs.

The kidney is generally weakly bilobed with an elongate pericardial lobe. In *Ngairea murphyi* (Fig. 10e) and some species of *Rhophodon* (Figs 27f, 30e) the rectal lobe is almost entirely absent and the pericardial lobe is markedly elongate. All these species have above average whorl counts. Bilobed kidneys with almost equal sized lobes are present in *Egilomen* (Figs 129d, 132f), *Sinployea intensa* (Fig. 138f) and *Letomola contortus* (Fig. 69g). Species of *Cralopa* (Figs 96e, 99e, 102e) have the rectal lobe about 1/3 the length of the pericardial lobe.

A mantle gland is usually present although no gland was noticed in *Hedleyoconcha*, *Sinployea* and some species of *Gyrocochlea*, *Nautiliropa*, *Elsothera* and *Rotacharopa*.

GENITAL ANATOMY

Ovotestis - Usually the ovotestis consists of two clumps of palmately clavate to finger-like lobes of alveoli embedded in the apical whorls of the digestive gland and oriented parallel to the plane of coiling. In species with an elevated spire such as those belonging to *Ngairea*, *Hedleyoconcha* and *Lenwebbia* the lobes are positioned at right angles to the plane of coiling (Figs 5c, 10g, 24e, 27d, 30c). *Gyrocochlea vinitincta* which has a greatly enlarged shell with expanded whorls, also has the ovotestis more at right angles than parallel (Fig. 46c).

Although two clumps of alveoli are normally present, some proliferation of clumps takes place in the high spired and high whorled *Ngairea murphyi* (Fig. 10d), and *Hedleyoconcha delta* (Fig. 24c). Single clumps are present in the tiny *Sinployea intensa* (Fig. 138c) and *Letomola contortus* (Fig. 69c) while according to Solem (1983, p. 74) a single clump is present in the minute *Discocharopa aperta*. Within a clump of the ovotestis the number of alveolar lobes varies from many in some of the larger species to the simple bilobed condition in the very small *Omphaloropa varicosa* (Fig. 135c), *Rhophodon bairnsdalensis* (Fig. 91d) and *L. contortus* (Fig. 69d). In *Rotacharopa* the ovotestis consists of two teardrop-shaped lobes (Figs 141c, 144c, 147c) representing a significant difference from the simple clavate alveoli in the Charopinae.

Hermaphroditic Duct - Most species investigated have a hermaphroditic duct which is a simple tube leading apically from the carrefour region, along the parietal whorl margin to the ovotestis located in the apical whorls of the digestive gland. In several species the tube is partially kinked. This is best illustrated in species of *Hedleyoconcha* (Figs 24d, 27e) which have elevated, trochoidal shells, and also in *Ngairea dorrigoensis* and *Gyrocochlea vinitincta* (Figs 4d, 46d). Differences in the degree of duct expansion, noted in some dissections, are most probably related to levels of reproductive activity and have little phyletic relevance. The colour of the duct varies from iridescent pink to iridescent green.

Talon and Carrefour - In a number of cases poor preservation made interpretation of this region difficult. Typically the talon is a circular to subcircular swelling situated atop a short stout stalk although in some species e.g. *Hedleyoconcha delta*, the talon is finger-like (Fig. 27c). Elongation of the talon stalk occurs in *Gyrocochlea curtisiana* (Fig. 55e), *Rhophodon bairnsdalensis* (Fig. 91e) and *Rotacharopa densilamellata* (Fig. 147d), while in *Sinployea intensa* and *Egilomen cochlidium* the stalk is extremely short (Figs 138c, 129c). The carrefour is typically an expansion in the talon stalk at its junction with the hermaphroditic duct.

Albumen Gland - The size of the albumen gland is variable and probably reflects the level of reproductive activity. Shape of the gland is affected largely by the degree of indentation by the spermathecal head and intestinal loops.

Prostate and Uterus - No species showed any departure from the typical charopid pattern of fused prostate-uterus. The prostatic alveoli are situated either along the full length of the uterine chambers or compacted into a mass at the base of the albumen gland (Fig. 115a).

The uterus consists of a lower chamber with thick walls thrown into folds and a thinner, glandular-walled upper chamber. In some cases this differentiation was externally conspicuous while in others, dissection was necessary to determine the areas of differentiation.

Terminal Male Genitalia - Differences in this region include relative size and shape variation in the vas deferens, epiphallus and penis; shifts in the insertion of the penial retractor muscle; modification of the vas deferens-epiphallus junction; positional variation in the epiphallus-penis junction; addition of structures; and major changes in the penis interior particularly under conditions of sympatry. Because of differences in preservation states between individual specimens, size and shape variations were not quantified.

The penial retractor muscle is generally a short tuft originating on the diaphragm and inserting on the epiphallus near or at the epiphallus-penis junction. The muscle is elongate in *Biomphalopa recava* and *Rhophodon consobrinus* but differential contraction of individual specimens did not enable full investigation of length differences. Major departures from this basic pattern include the shift of the insertion point onto the penis head or to a point well along the epiphallus. The former condition is usually associated with a shift of the epiphallic entrance to a sub-apical position on the penis e.g. *Ngairea murphyi* (Fig. 10b), *Rhophodon consobrinus* (Fig. 75c), *Gyrocochlea* and *Biomphalopa* (Figs 46b, 49b, 52b, 55a, 58b, 61b). In *Egilomen globosa* (Fig. 132b), and *Cralopa kaputarensis* (Fig. 99b), the penial retractor muscle inserts c. 1/3 of the way along the epiphallus while in *Setomedea nudicostata* (Fig. 36b), and *Elsothera genithecata* (Fig. 109a), the insertion point is c. 1/2 way along the epiphallus. In *Rotacharopa*, the epiphallus is differentiated into ascending and descending arms and the retractor muscle is inserted either at the point of reflexion (Figs 144a, 147a), or at the vas deferens-epiphallus junction (Fig. 141a). This latter shift in position may be related to the effects of increased whorl count.

An unusual condition in *Setomedea monteithi* (Fig. 42a), and *Gyrocochlea curtisiana* (Fig. 55a) has retractor muscle and terminal part of epiphallus intertwined.

The vas deferens is typically a thin tube descending from the prostate-uterus to the penioviducal angle before reflexing and giving rise to a more expanded epiphallus c. 1/2-1/3 of the way along the penis length. Exceptions are *Gyrocochlea* which has the vas deferens expanded initially before becoming more slender prior to joining the epiphallus (Figs 46a, 49a, 55a), and *Cralopa* which has the vas deferens expanded for its entire length (Figs 96a, 99a, 102a). In most species the vas deferens enters the epiphallus apically through a simple pore, however in *Elsothera sericatula* (Fig. 105b) and *E. genithecata* (Fig. 109a), the vas deferens enters the epiphallus laterally through a large cup-shaped pilaster. Externally this complex junction is a conspicuous swelling.

The epiphallus is usually differentiated from the vas deferens as an abruptly expanded, muscular tube, generally shorter than the penis, internally with longitudinal pilasters, and reflexed before entering the penis apically. Departures from the general pattern include *Gyrocochlea* which has an epiphallus that is as long as the penis (Figs 46a, 49a, 52b, 55a), and *Ngairea murphyi* (Fig 10a), *Rhophodon kempseyensis* (Fig. 79a), *Elsothera genithecata* (Fig. 109a), *Ngairea canaliculata* (Fig. 13a), *Setomedea nudicostata* (Figs 36a,b), and *Coenocharopa sordidus* (Fig. 112a), which have an epiphallus that is much longer than the penis. In *R.*

kempseyensis and *N. murphyi* the elongate epiphallus may be a secondary modification related to whorl count increment; in *C. sordidus* the change to longer epiphallus occurs under conditions of complex congeneric sympatry and may be associated with species recognition; in *E. genithecata* the enlarged epiphallus correlates with overall size increase.

Letomola contortus, which has reduced whorl count, has elongate terminal genitalia with long slender epiphallus and penis of equivalent length (Fig. 69a). However, the bulbous protoconch indicates descent from a larger ancestor and elongation in this case can be interpreted as secondary miniaturisation of a larger genital system.

The epiphallus undergoes minor structural modification in *Setomedea seticostata* which has the terminal part of the epiphallus and apical section of the penis bound in a connective sheath (Fig. 33a,b), and *S. janae* which has the epiphallus incorporated into the penial apex (Fig. 39a,c). *Gyrocochlea*, *Coenocharopa macromphala* (Fig. 115a), and *C. alata* (Fig. 118b), have the terminal portion of the epiphallus bound to the penis sheath with thin strands of connective tissue. In *Elsothera genithecata* a thick muscular sheath covers the terminal half of the epiphallus and the penial retractor muscle is inserted on the sheath (Fig. 109a). In contrast to the minor adjustments seen in *Setomedea* and *Coenocharopa* the epiphallic sheath of *E. genithecata* represents a major additive structure.

A more significant deviation from the above patterns is seen in *Rotacharopa* where the epiphallus has ascending and descending arms of roughly equal length but with the latter greatly expanded. The penial retractor muscle is inserted either at the point of reflexion or at the vas deferens-epiphallus junction (Figs 141a, 144a, 147a). This external change correlates with a significant change in internal structure. Typically the interior walls of the epiphallus are sculptured with simple longitudinal thickenings whereas in *Rotacharopa* there are large transverse thickenings (Figs 141b, 144b).

Entry of the epiphallus into the penis is usually apical, through a simple pore surrounded by a circular fleshy thickening or two fleshy lips. In *Gyrocochlea*, *Biomphalopa* and some *Setomedea*, the entry point is in a subapical position, with the penial retractor muscle inserted on the penis head (Figs 33c, 49b, 52b, 58b). These positional shifts are associated with elongation of the penis (*Gyrocochlea*, *Biomphalopa*) or change in epiphallus structure (*Setomedea*) and are in contrast to the positional shifts related to increased whorl count in *Nguirea murphyi* (Fig. 10b) and species recognition in *Rhophodon consobrinus* (Fig. 75c). Conical verges are developed in *Gyrocochlea vinitincta* (Fig. 46b) and *Ngairea canaliculata* (Fig. 13b), most probably in response to congeneric sympaters. A tubular verge is seen in *Omphaloropa varicosa* (Fig. 135b).

The penis is generally a short, muscular tube which may have an apical section expanded in response to complex internal pilasters or incorporation of the epiphallus. Exceptions include the elongate, sometimes reflexed, cylindrical penis of *Gyrocochlea* (Figs 46a,b, 49a,b), expanded, barrel-shaped penis of *Cralopa* (Figs 96a, 99a, 102a), and tubular penis of *Coenocharopa* (Figs 115a, 118a, 124a). A more drastic change is seen in the penis of *Rotacharopa* which has the typical apical bulb of other charopids and an unusual basal extension. This basal extension, or preputial tube as it is here named, is most noticeable in *R. densilamellata* (Fig. 147a), where it is almost twice the length of the penis proper. Function of this structure is unknown.

A penis sheath is present in *Gyrocochlea*, *Coenocharopa* and some species of *Rhophodon*.

The penis interior is variable between genera; and within genera under conditions of congeneric sympatry. However, there is generally an apical epiphallic pore and basal longitudinal pilasters, sometimes with a muscular apical collar separating the penial bulb from the lower tubular section.

In *Ngairea* a muscular collar below the epiphallic entrance effectively divides the penis into two chambers (Figs 4b, 10b, 13b, 16b), while *Hedleyoconcha* has a grooved muscular thickening constricting the passage between the epiphallic pore and the basal portion of the penis (Figs 24c, 27b). The shift in epiphallic entrance to a subapical position in *Setomedea seticostata* (Fig. 33c), *S. monteithi* (Fig. 42c), and *Rhophodon consobrinus* (Fig. 75c) has resulted in the development of an apical penial chamber which has developed its own pilaster structure, most likely for species recognition. In contrast *Ngairea murphyi* which also has a subapical epiphallic entrance has an apical penial chamber without pronounced sculpture (Fig. 10b). *Nautiliropa omicron* which has a penis with an apical bulb separated from the main chamber by a thin muscular collar (Fig. 65c) also has the epiphallic entrance apical, though slightly lateral, with the penial retractor muscle inserted on the penial bulb. In addition to the epiphallic entrance the penial bulb contains a horseshoe-shaped pilaster. This pattern is broadly equivalent to that seen in *S. seticostata* and *R. consobrinus.*

Elsothera sericatula (Fig. 105c) and *E. genithecata* (Fig. 109b), have penes which are also internally divided by a muscular collar. The epiphallic entrance is apical and the region between the collar and the epiphallic pore is large and sculptured with short fleshy thickenings. This change to two quite differently sculptured penial chambers in *Elsothera* is a major structural change and contrasts with some of the species recognition changes mentioned previously.

In *Gyrocochlea*, the long, cylindrical penis is internally differentiated into a lower portion with large, longitudinal pilasters and an area apicad of the simple epiphallic pore which has short, almost pustular, thickenings (Figs 49a, 52a). The exception is *G. vinitincta* with a conical verge (Fig. 46a). *Biomphalopa recava* has a single large longitudinal pilaster and short longitudinal thickenings apicad of the epiphallic pore (Fig. 58b) but *B. concinna* lacks the apical thickenings and has a well-developed spatulate verge (Fig. 61b). Verges are also present in *Setomedea nudicostata*, *Omphaloropa varicosa*, and *Rotacharopa kessneri* (Figs 36b, 144b).

The penis is typically sculptured with intergenerically-variable longitudinal pilasters which show marked intrageneric differences under conditions of sympatry. These differences may be subtle minor shifts in size and shape of pilasters as in *Gyrocochlea*, *Ngairea* and *Setomedea*, or may involve more drastic alteration of pilaster patterns as seen in *Rhophodon*, *Coenocharopa*, *Egilomen* and *Rotacharopa*. *Gyrocochlea vinitincta* and *G. paucilamellata*, are sympatric in areas of the Lamington National Park in the eastern Border Ranges, SEQ. *G. paucilamellata* retains the typical generic pattern of numerous anastomosing longitudinal pilasters (Fig. 52b) while *G. vinitincta* has an altered condition in which the pilasters are simple and unbranched (Fig. 46b). This change may seem minor but, together with the conical verge of *G. vinitincta*, would serve as an effective species isolating mechanism. The microsympatric *Ngairea corticicola* and *N. dorrigoensis* have numerous longitudinal pilasters, but these are strongly corrugated in *N. corticicola* (Fig. 16b) and simple in *N. dorrigoensis*. In *Setomedea monteithi*, which is probably sympatric with *S.* sp., short longitudinal pilasters are replaced by two short pad-like pilasters (Fig. 33c).

More dramatic pilaster pattern alteration is seen in *Coenocharopa sordidus* and *C. yessabahensis*. Sympatry in *Coenocharopa* is highly complex with two to three species involved per locality. In *C. yessabahensis* an apical pad and large semi-circular basal pilaster (Fig. 124b) replace the more typical longitudinal pattern (Figs 115d, 118b), while the horseshoe-shaped pilasters of *C. sordidus* represent further variation (Fig. 112a).

In *Rhophodon* pilasters are typically fusiform longitudinal. *R. peregrinus* has a penis with an apical verge-like thickening and basal circular pilaster (Fig. 72b), while the sympatric *R. consobrinus* has longitudinal pilasters in the penis proper, a basal circular pilaster and shift in epiphallic entry (Fig. 75e). The two species of *Egilomen* are sympatric and have quite contrasting patterns of penial surface sculpture (Figs 129b, 132b).

In the three species of Rotadiscinae the change from typical longitudinal pilasters to the pad-like pilasters of *Rotacharopa annabelli* (Fig. 141b), is an equivalent change to that seen among members of sympatric species pairs in the Charopinae. However a sympatric partner for this species has yet to be found.

Of the monotypic genera, *Lenwebbia* and *Omphaloropa* have simple longitudinal pilasters (Figs 30b, 135b); *Letomola* has an apical spongy thickening in addition to longitudinal pilasters (Fig. 69b); and the penis of *Sinployea intensa* was too poorly preserved to accurately detail internal features, though a basal semicircular pilaster (Fig. 138b) relates to the generic pilaster pattern (Solem, 1983).

In *Nautiliropa omicron* the penis has several anastomosing longitudinal pilasters and a large apical pocket stimulator (Fig. 65c). This contrasts with the conchologically similar *Gyrocochlea*, and effectively separates *Nautiliropa* and *Gyrocochlea*. The complex stimulator is different to the simple circular and pad-like pilasters developed in other genera discussed above and indicates that it probably is not a simple species recognition feature.

Terminal Female Genitalia - Observed variation was confined to differences in the comparative lengths of the free oviduct and vagina. The few species in which the internal wall sculpture was examined showed a repetitive pattern of longitudinal pilasters; no attempt was made at detailed analysis as presented for male genitalia. Length of structures may be affected by contraction during preservation so comparisons are presented qualitatively rather than quantitatively.

In general, genera with elongate genitalia have long vaginae e.g. *Hedleyoconcha*, *Gyrocochlea*, *Letomola* and *Rhophodon* (Figs 24a, 46a, 69a, 72a). However, length changes in the vagina may also be related to species recognition. *Rhophodon consobrinus* with short vagina (Fig. 75a) in comparison with its congeners, is sympatric with *R. peregrinus* and has altered terminal male genitalia. *Coenocharopa*, except *C. sordidus* (Fig. 112a), has average length vaginae; *C. sordidus*, which exists under conditions of complex congeneric sympatry, has a very short vagina. Short vaginae are also present in *Ngairea* and *Lenwebbia* (Fig. 30a).

The free oviduct is typically a muscular tube equal in length to, or only slightly longer than, the vagina. Conspicuous exceptions are *Ngairea* (Figs 4a, 13a), *Rhophodon consobrinus* (Fig. 75a) and *Coenocharopa sordidus* (Fig. 112a), which have much longer free oviducts.

Atrium - The atrium does not display any unusual features apart from minor variations in length. The shortened condition in *Rhophodon consobrinus* (Fig. 75a) and the elongate structure in *Coenocharopa sordidus* (Fig. 112a) illustrate the extent of variation.

Spermatophore - Sperm packets were found in five species. The most unusual spermatophore was that of *Setomedea monteithi*, which had a long chitinous tail (Fig. 42b). The others consisted of a clavate structure in *Nautiliropa omicron* (Fig. 65d), an arc-shaped, terminally hooked packet in *Gyrocochlea paucilamellata* (Fig. 52d), and a vaguely U-shaped packet in *Rhophodon consobrinus* and *R. kempseyensis* (Figs 75f, 79f). Although few were located, it is probably more than coincidental that the two *Rhophodon* species have similar looking spermatophores.

Radula

The usual pattern of radular structure is for a tricuspid central tooth, slightly smaller than the adjacent laterals, with long, lanceolate mesocone and short pointed ectocones; tricuspid lateral teeth which are similar in shape to the central; a transition zone of lateromarginal teeth in which the endocone becomes curved and elongate, the mesocone becomes shorter and the ectocone lengthens slightly; and marginals in which the endocone and mesocone are reduced, and the ectocone, and occasionally the endocone, are split into a series of minor cusps. *Setomedea nudicostata* is typical (Fig. 35d,g,h).

Variations fall into several categories. Minor differences in the size and shape of teeth occur in *Biomphalopa* and *Gyrocochlea* which have a slightly more elongate mesocone on the central and lateral teeth (Figs 45g, 48d, 57d). *Elsothera* has a large, broadly lanceolate mesocone on the central and lateral teeth (Figs 104g; 108g,h); *Egilomen* and *Cralopa* have the central tooth c. 1/2 the size of the laterals (Figs 98f, 101f, 128h, 131h); *Omphaloropa* has a small central tooth and reduced number of teeth per row (Fig. 134d,h): *Rotacharopa* and *Rhophodon* have slender, lanceolate mesocones on the lateral and central teeth (Figs 146g, 190d). In contrast to the average generic pattern *Rhophodon kempseyensis* has the mesocone of the central and laterals greatly expanded (Fig. 78e). This condition is also seen in *Coenocharopa yessabahensis* (Figs 123d,h). Significantly both *R. kempseyensis* and *C. yessabahensis* live on limestone rocks and the modification in cusp size probably relates to an associated shift in feeding habit.

A more dramatic level of change in tooth shape is seen in *Letomola contortus* (Fig. 68d,e,f) and *Nautiliropa omicron* (Fig. 63c,f). *L. contortus* has a highly modified radula with a small central tooth which has the side cusps reduced to tiny knobs. In contrast, the first row of laterals has a greatly enlarged, broadly lanceolate mesocone and small side cusps. Furthermore there are very few lateral teeth, no transitional lateromarginal teeth, and serrate marginals (Fig. 68d). *L. contortus* lives on limestone and the enlarged mesocone on the laterals may be habitat related. However, the remaining modifications are major changes in radular structure which correlate with the many unusual conchological specialisations. In *N. omicron* the central and inner laterals have a long, slender, curved mesocone and almost obsolete side cusps (Fig. 63f), the outer laterals have the endocone lengthened and curved, and the marginals are unusual in having an elongate basal shaft with two cusps - the mesocone and endocone - in a crab-claw arrangement (Fig. 63c). The teeth are arranged in V-shaped rows as opposed to the straight line arrangement in other genera. These features are significantly different to the typical pattern of other log-dwelling species reviewed.

Some unusual radular variations also occur among species with an incomplete secondary ureter. *Lenwebbia protoscrobiculata* has typical central, lateral and marginal teeth but lacks transitional lateromarginal teeth (Fig. 29d). *Hedleyoconcha delta* has a typically tricuspid central tooth, but with a marked flare of the basal plate (Fig. 23g); the flared extension is less obvious in the lateral and marginal teeth. *Mussonula fallax* (Fig. 20d,e), has a tricuspid central tooth with a broad anterior extension, laterals initially bicuspid, outer laterals and lateromarginals tricuspid with the basal extension further enlarged, and marginals typically multicuspid with an enlarged basal extension. A similar pattern is present in the conchologically convergent *Ngairea levicostata*, although, the basal extension is more pronounced (Fig. 6f). In *N. murphyi* the basal extension is absent in the central tooth but present as a conspicuous outwardly directed flare in the laterals (Fig. 9d,h).

Ngairea corticicola, *N. dorrigoensis* and *N. canaliculata* have radulae with a small, broadly triangular central tooth with a short broad basal extension, and laterals and marginals with a distinctly flared extension (Figs 3f, 12d, 15d,h).

These changes to tooth structure in *Mussonula*, *Hedleyoconcha* and *Ngairea* represent a change in interrow support which in *Hedleyoconcha* and *Ngairea* correlates with a shift to semiarboreal and arboreal lifestyles. The preferred microhabitat of *Mussonula* is unknown.

SUMMARY

It is possible to group the conchological and anatomical patterns outlined above, into levels of evolutionary significance (Solem, 1978). At the lower end of the scale there are changes which are related to species recognition. These include differences in the internal sculpture of the penis, minor positional shifts in terminal reproductive structures, and differences in shell morphology and radular structure associated with small habitat shifts. Examples are given in species accounts. At a slightly higher level are those changes associated with colonising particular adaptive zones. These include the periostracal setae of the damp habitat *Setomedea*; the reduced sculpture of the interstitial *Coenocharopa*; the strongly to moderately elevated shells of the semiarboreal and arboreal *Hedleyoconcha*, *Lenwebbia* and *Ngairea*; the strongly ribbed, flattened to biconcave shells of the under-log dwelling *Gyrocochlea*, *Nautiliropa* and *Biomphalopa*; the dentate, sculptured shells of the rock dwelling *Rhophodon*; and the dentate, secondarily modified shell of rock dwelling *Letomola*. Corresponding anatomical changes include alterations in penis shape and internal penial structure, addition of major structures to the genitalia, changes in kidney shape, and radical modifications in radular morphology. Above this level are basic changes in sculptural elements and large scale changes in anatomy, such as in *Rotacharopa* and possibly the group of genera with incomplete secondary ureter.

SYSTEMATICS

Family CHAROPIDAE Hutton, 1884

Solem (1983, p. 59) presented a detailed diagnosis that is accepted herein.

Subfamily CHAROPINAE Hutton, 1884

A broad definition of the subfamily is presented by Solem (1983, p. 70). The genitalia of the Charopinae reviewed here show a consistent pattern of muscular epiphallus with internal longitudinal thickenings, reflexed before entering the penis through a simple pore, or occasionally a verge. The penis has an apical bulb containing the epiphallic entrance and a lower basal portion with longitudinal thickenings which may be modified under conditions of sympatric species interaction. The pallial configuration includes a kidney in which the pericardial lobe is usually much longer than the rectal lobe and the secondary ureter is complete or rarely incomplete.

Ngairea gen. nov.

Oreokera Iredale, 1933 (part), p.54, nom. nud.; Iredale, 1937a (part), p. 318, nom. nud.; Iredale, 1941a, p. 261, nom. nud.; non Stanisic, 1987, p.2.

ETYMOLOGY

For my youngest daughter Ngaire.

TYPE SPECIES

Oreokera dorrigoensis Iredale, 1941.

PREVIOUS STUDIES

Iredale (1933) introduced *Oreokera* for *Flammulina cumulus* Odhner, 1917 and added *Helix corticicola* Cox, 1866 (Iredale 1937a) and *Ore*-

okera dorrigoensis Iredale, 1941. Stanisic (1987) validated *Oreokera*, including only *F. cumulus*, and one other north Queensland species. *Ngairea* is introduced to include *H. corticicola*, *O. dorrigoensis*, two new species from southern Queensland, and '*Helix*' *murphyi* Cox, 1864 from southern NSW. The latter was previously included in the punctid form-group *Paralaoma* Iredale, 1913 by Iredale (1937a, 1941a).

DIAGNOSIS

Large to very large, diameter 5.46–7.40 mm, with 4 1/8 to 5 7/8 normally to tightly (*murphyi*) coiled whorls. Height 2.86–5.35 mm. Apex and spire moderately to strongly (*murphyi*, *levicostata*) elevated, body whorl descending slightly. Protoconch almost flat, 1 5/8 to 1 3/4 whorls. Apical sculpture of curved radial ribs, reduced (*canaliculata*) or modified (*murphyi*), with incised spiral grooves (*canaliculata*, *corticicola*), weak raised spiral cords (*levicostata*) or without spiral elements (*dorrigoensis*, *murphyi*). Post nuclear sculpture of crowded, protractively sinuated radial ribs which may be reduced in some species (*corticicola*). Microsculpture of crowded spiral cords (*murphyi*, *dorrigoensis*), incised spiral grooves (*corticicola*, *canaliculata*), or fine spiral lines (*levicostata*). No microriblets present. Sculpture continuous on the base but reduced. Umbilicus narrow to widely U-shaped (*murphyi*), rarely closed (*dorrigoensis*). Sutures impressed, maybe channelled (*canaliculata*). Whorls weakly angulate to strongly carinate (*murphyi*), sometimes rounded (*canaliculata*). Aperture roundly lunate to subquadrate. Lip simple, sometimes slightly thickened; columella vertical, reflected toward umbilicus. Colour yellow-horn, with red flammulations or without (*murphyi* and *canaliculata*.)

Foot and tail broad, bluntly rounded posteriorly; a caudal horn sometimes present (*levicostata*). Animal creamy-white with orange-grey speckling on the sides of the foot and on the mantle collar. Pallial roof and visceral hump with variable black speckling. Ommatophores black. Kidney broadly to narrowly (*murphyi*) triangular; rectal lobe vestigial or absent (*murphyi*). Ureter sigmurethrous with incomplete secondary branch. Ureteric opening at the rear of the pallial cavity in the angle between kidney and hindgut. Genitalia with ovotestis of two or more (*murphyi*) clumps of palmately clavate lobes of alveoli, separated by digestive gland and oriented at right angles to the plane of coiling. Terminal male genitalia with muscular epiphallus, sometimes much longer (*canaliculata*) than the penis, entering the penis apically, or subapically (*murphyi*). Epiphallic pore central in muscularised pilaster or opening through a conical verge (*canaliculata*). Penial retractor muscle inserted on the epiphallus (*dorrigoensis*), penis-epiphallus junction (*corticicola*, *canaliculata*), or on the penis (*murphyi*). Penis with an apical bulb internally separated from a lower tapered, tubular section by a muscular collar. Internal penial sculpture of broad, corrugated (*corticicola*, *canaliculata*) or slender (*murphyi*, *dorrigoensis*) fleshy, longitudinal pilasters. Female reproductive tract without unusual features.

Central tooth of radula broad, triangular with tiny ectocones, or slender lanceolate (*levicostata*, *murphyi*) with prominent ectocones.

DISTRIBUTION AND ECOLOGY

Ngairea extends from warm temperate closed forests in the Illawarra region of southern NSW to the subtropical and temperate rainforests of northern NSW, and drier subtropical forests of southern Queensland. With the exception of *N. murphyi* and *N. levicostata* species distributions are well known. Most species live under the bark of fallen trees.

N. corticicola is sympatric with *N. dorrigoensis* from Dorrigo to the eastern Border Ranges; *N. levicostata* is sympatric with *N. dorrigoensis* in the Koreelah State Forest region of the western Border Ranges. *N. dorrigoensis* and *N. corticicola* were collected from under the same piece of bark at Upper Pine Creek, Canungra, SEQ. In *N. dorrigoensis* and *N. levicostata* differences in shell shape and radula indicate divergent microhabitat preferences.

PATTERNS OF SHELL VARIATION

Size and Shape - Adult *Ngairea* are some of the largest Australian subtropical charopids with mean shell diameter 5.80–6.90 mm. Average whorl counts range from 4 1/2- to 5 1/2-. *N. murphyi* has the highest mean whorl count (5 1/2-), smallest mean diameter, but has a smaller whorl cross section.

Reduced height in *N. murphyi* is the result of smaller shell size but *N. levicostata* has a taller shell through spire elevation. In *N. murphyi* and *N. dorrigoensis* decreased shell height correlates with keel development on the body whorl.

The umbilical opening is smallest in species with a distinctive keel (*N. dorrigoensis* and *N.

levicostata) although *N. murphyi* has a secondarily enlarged umbilicus resulting from reduction in size of whorl cross section.

Sculpture - Apical sculpture consists of curved, crowded radial ribs which may be pronounced, reduced or modified into vague radial ridges and wrinkles. Less prominent spiral elements may be present as incised spiral lines or raised cords. In *N. corticicola* (Fig. 15e) intersections of radials and spirals form a series of pits.

Postapical sculpture is predominantly radial, with ribs varying from bold, broad, regularly spaced (Fig. 12a), and high, crowded (Fig. 6e) to very crowded (Figs 3e, 9g). Various types of spiral sculpture are also present and in *N. corticicola* (Fig. 15f), incised spiral lines become notched, approximating some helicarionid taxa, e.g. *Westracystis* Iredale, 1939 and *Delinitesta* Iredale, 1933 (Solem, 1982; Stanisic, 1988).

One of the more interesting developments in the shell of *Ngairea* is the canalised sutures seen in *N. canaliculata*. Solem (1983, pp. 9, 108) recorded this feature in the Pacific Island charopid *Sinployea proxima* (Garrett, 1872). Canalisation is due to detachment of part of the body whorl and in *N. canaliculata* results in a relatively wide channel.

Variation in shell morphology is greater than in other genera included in this study indicating a long, complex period of evolution. *N. murphyi*, which has developed in isolation from the main group of species exhibits some major departures from average patterns.

PATTERNS OF ANATOMICAL VARIATION

Variations in anatomy involve shape changes in the pallial structures, size differences in reproductive organs, species interaction modifications in the terminal male genitalia, and diet related shifts in radular morphology.

COMPARISONS

Ngairea and *Mussonula* may be confused and are sympatric in and around the eastern part of the Border Ranges. *Mussonula* has a strongly exsert protoconch with prominent spiral cords and vague radial ridges prominent toward the nuclear-post nuclear shell boundary (Figs 18d, 20f). *Lenwebbia* is sympatric with *Ngairea* between Colosseum Creek and the Bobby Range, SEQ, and bears some similarity. However, it has a strongly punctate protoconch, adult sculpture of spiral grooves and fine thread-like radials (Fig. 29e–g), lacks the internal division of the penis, and has the kidney apex divided by a portion of reflexed ureter (Fig. 30b,e).

KEY TO SPECIES OF *NGAIREA*

1.Shell with prominent radial ribs 2

Shell without prominent radial ribs; base almost smooth (Fig. 15b) .... *corticicola*

2.Sutures simple 3

Sutures channelled (Fig. 12e) .... *canaliculata*

3.Umbilicus nearly closed to slightly open; peripheral keel obtuse 4

Umbilicus widely open (Fig. 9b); peripheral keel acute (Fig. 9c) .... *murphyi*

4.Microsculpture of prominent spiral cords (Fig. 3e); spire lower, mean H/D ratio 0.56 .... *dorrigoensis*

Microsculpture of weak spiral lines (Fig. 6e); spire higher, mean H/D ratio 0.73.................. ....*levicostata*

Ngairea dorrigoensis (Iredale, 1941) comb. nov.(Figs 3–5; Tables 2, 3)

Flammulina corticicola (Cox); Hedley, 1912 (part), p. 264, pl. 7, figs 46-48.
Oreokera dorrigoensis Iredale, 1941a,p. 265, fig. 5

COMPARISONS

N. dorrigoensis differs from *N. corticicola* in its more prominent radial sculpture, more angulate periphery, narrower umbilicus and microsculpture of crowded microspiral thickenings (Fig. 3e). *N. levicostata* has a more elevated shell and microsculpture of fine spiral lines (Fig. 6e). The apical spiral cords, smaller size and lack of prominent spiral cords on the adult whorls of *Mussonula* Iredale, 1937 readily separate members of that genus from *N. dorrigoensis*.

TYPE MATERIAL

HOLOTYPE: AMC63517, Dorrigo Scrub, NSW., Height of shell 3.45 mm, diameter 6.23 mm, H/D ratio 0.55, D/U ratio 14.49, whorls 4 1/2-.
PARATYPE:AMC63513, same locality as holotype.

TABLE 2–RANGE OF VARIATION IN *NGAIREA*, *MUSSONULA*, *LENWEBBIA* AND *HEDLEYOCONCHA* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Ngairea durrigoensis	16	4 3/4 (4 1/8-5 1/8)	3.78 (3.36-4.62)	6.50 (5.71-7.40)	0.58 (0.52-0.64)	0.62 (0.42-0.92)	2.10 (1.93-2.44)	0.31 (0.17-0.39)	---	--	0.46 (0.30-0.68)	14.59 (9.26-21.83)
Ngairea levicostata	2	4 1/2- (4 1/4-to4 5/8)	4.37 (3.95-4.79)	5.97 (5.63-6.30)	0.73 (0.70-0.76)	0.64 (0.67-1.01)	2.06 (1.85-2.27)	0.40 (0.36-0.44)	---	--	0.46 (0.45-0.47)	12.91 (12.46-13.35)
Ngairea murphyi	4	5 1/2- (5 - 5 7/8)	3.24 (2.96-3.70)	5.60 (5.46-6.05)	0.56 (0.49-0.63)	0.71 (0.50-1.09)	1.62 (1.60-1.66)	0.44 (0.32-0.65)	---	--	1.39 (1.28-1.58)	4.17 (3.84-4.39)
Ngairea canaliculata	21	4 5/8- (4 1/2-4 3/4)	3.83 (3.28-5.35)	6.51 (5.97-7.39)	0.59 (0.53-0.83)	0.51 (0.34-0.67)	2.15 (1.93-2.27)	0.24 (0.18-0.32)	---	---	0.71 (0.43-0.94)	9.40 (7.21-15.61)
Ngairea corticicola	34	4 3/4+ (4 3/8-5 1/2)	3.90 (3.36-4.62)	6.90 (5.88-7.82)	0.56 (0.50-0.63)	0.67 (0.42-0.92)	2.11 (1.93-2.15)	0.31 (0.22-0.39)	---	--	0.81 (0.55-1.02)	8.61 (6.99-11.31)
Mussonula verax	4	4 - (3 7/8-4+)	4.31 (4.03-4.45)	5.36 (5.04-5.63)	0.81 (0.79-0.82)	0.99 (0.92-1.06)	1.83 (1.77-1.91)	0.54 (0.52-0.57)	104.75 (90-120)	6.20 (5.68-6.78)	0.35 (0.31-0.41)	15.27 (13.29-17.19)
Mussonula fallax	2	4 1/8-	3.37 (3.32-3.41)	5.07 (4.81-5.32)	0.67 (0.64-0.69)	0.68 (0.64-0.72)	1.62	0.42 (0.39-0.45)	---	--	0.84 (0.82-0.86)	6.02 (5.86-6.18)
Lenwebbia protoverobiculata	24	4 1/8+ (3 7/8-4 3/8+)	2.79 (2.36-3.15)	4.35 (3.96-4.69)	0.64 (0.61-0.71)	0.45 (0.30-0.68)	2.34 (2.13-2.68)	0.19 (0.12-0.28)	---	---	0.75 (0.62-0.82)	5.85 (5.34-6.52)
Hedleyoconcha delta	20	6 1/8+ (5 7/8-to6 5/8)	6.01 (5.04-7.90)	7.77 (6.22-10.08)	0.78 (0.71-0.88)	1.73 (1.26-2.35)	2.60 (2.35-2.94)	0.66 (0.36-0.88)	---	--	0.89 (0.62-1.54)	9.01 (6.55-11.28)
Hedleyoconcha ailaketoae	2	5 1/8 (5 1/8-5 1/8+)	4.88 (4.62-5.13)	6.39 (5.97-6.81)	0.76 (0.75-0.77)	1.39 (1.35-1.43)	2.27	0.61 (0.59-0.63)	---	--	0.72	8.89 (8.30-9.47)

OTHER MATERIAL

NEW SOUTH WALES: Platypus Creek, New England N.P., (1 AMC142440, 27 Feb 1961, D.F. McMichael); Acacia Plateau Rd, c. 12.2 km from Acacia Ck - Killarney Road, SEVT/MVF (28°21'S, 152°24'E) (1, AMC128560, 15 Mar 1981, J. Stanisic, D. Potter); Beaury S.F., c. 15 km W of Urbenville, 810 m (28°27'S, 152°24'E) (3, AMC142475, 18 May 1976, P.H. Colman, I. Loch); Marengo S.F., c. 40 km NW of Dorrigo, 1020 m (30°06'S, 152°25'E) (5, AMC142476, 10 Feb 1976, J.B. Burch, P.H. Colman); SE of Tabulam, tributary of Busby's Creek (29°02'S, 152°43'E) (2, AMC137757, 29 Aug 1982, ABRS - AM/QM); The Glade, Dorrigo N.P., 600 m, temperate rainforest (30°22'20"S, 152°43'40"E) (1, QMMO16440, 12 Nov 1983, ABRS - AM/QM); Tooloom Scrub, Beaury S.F., CNVF (28°29'S, 152°24'E) (2, QMMO10939, 15 Mar 1981, ABRS - AM/QM); Dorrigo (6, AMC142443); Dorrigo, under bark and logs (1, AMC63788, Dec 1910, S.W. Jackson); Dorrigo (1, AMC142444, ex Helms); Moonpar S.F., Dorrigo (1, AMC142441, 4 Apr 1960, D.K. McAlpine); Booyang (= Booyong?) Richmond River (1, AMC5786, ex Hedley); Washpool S.F., SW of Casino, dry eucalypt forest (29°13'30"S, 152°29'E) (1, AMC136879, 29 Aug 1982, ABRS - AM/QM); Wonga Walk, The Glade, Dorrigo N.P., under bark of fallen tree, rainforest (30°22'S, 152°44'E) (1, QMMO17137, 6 Mar 1987, J. Stanisic, D. Potter); Mills Rd, Moonpar S.F., under bark of fallen tree, rainforest (30°13'S, 152°39'E) (1, QMMO17141, 7 Mar 1987, J. Stanisic, D. Potter).

SOUTH EAST QUEENSLAND: c. 1 km E of Carr's Lookout, Koreelah S.F., under bark of fallen tree, NVF (3, QMMO16470, 3 May 1986, J. Stanisic); Mt Glorious, litter, NVF (1, QMMO16130, 26 Jan 1986, J. Stanisic); Mt Glorious, c. 3 km SE of summit, NVF (27°20'S, 152°,46'E) (1, QMMO11992, 2 Dec 1982, ABRS - AM/QM); c. 28.5 km from Goomburra, Goomburra S.F., 600 m, CNVF/Palms (27°59'S, 152°21'E) (3, AMC136812, QMMO12690, 7 Dec 1981, ABRS - AM/QM); Fred's Road, Mt Mee, rainforest (27°05'S, 152°43'E) (2, QMMO16460, 14 Apr 1980, J. Stanisic, N. Hall, A. Green); Maiala N.P., Mt Glorious, litter (1, QMMO11852, 20 Jun 1982, MSA Party); Lower Ballanjui Falls circuit, Lamington N.P., litter, NVF (1, QMMO16448, 3 Oct 1986, J. Stanisic, D. Potter); Canungerah (= Canungra), pine scrub (5, AMC32997, Jul 1908, S.W. Jackson); Mt Tamborine (2, AMC142442); Maiala N.P., Mt Glorious, CNVF (1, QMMO6304, 1 Oct 1976, M.J. Bishop); Mt Mistake, Goomburra S.F., under bark of fallen trees, CNVF (2, QMMO16571, 5 May 1986, J. Stanisic); Running Ck, Lion's Road, via Rathdowney, under bark of fallen tree, rainforest near picnic area (2,

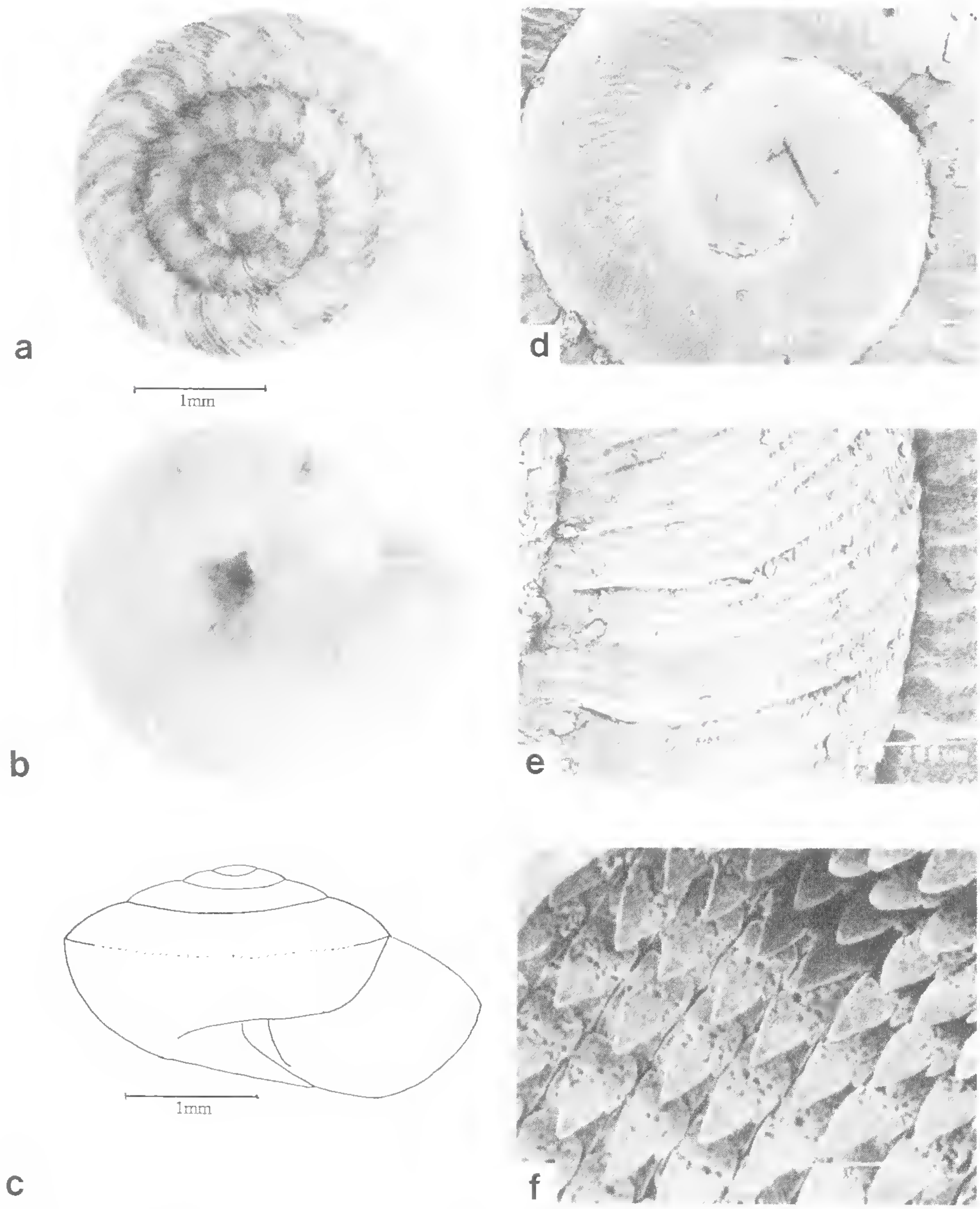


FIG. 3. *Ngairea dorrigoensis* (Iredale, 1941). a–c, Dorrigo Scrub, NSW. AMC63517, holotype; d–e, c. 1 km E of Carr's Lookout, Koreelah S.F., NSW. QMMO16470; f, Upper Pine Ck, Canungra, SEQ. QMMO16544. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, central (top left) and lateral teeth. Scale lines as marked.

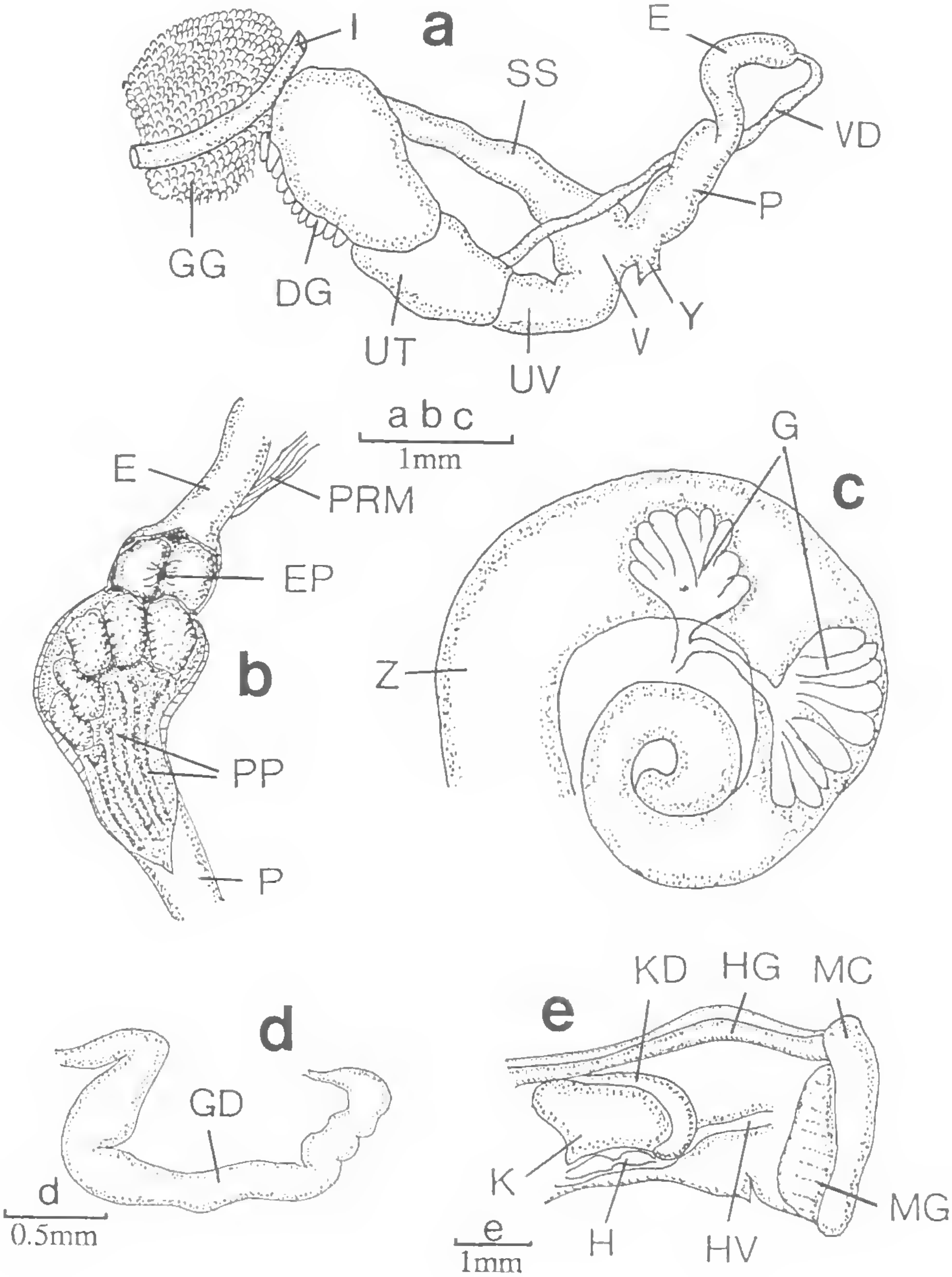


FIG. 4. *Ngairea dorrigoensis* (Iredale, 1941). a, c–e, Maiala N.P., Mt Glorious, SEQ. QMMO6304. b, Upper Pine Creek, Canungra, SEQ. QMMO16583. a, genitalia; b, details of penis interior; c, ovotestis; d, hermaphroditic duct; e, pallial cavity. Scale lines as marked.

TABLE 3 - LOCAL VARIATION IN *NGAIREA DORRIGOENSIS* (IREDALE, 1941), *NGAIREA LEVICOSTATA* SP. NOV. AND *NGAIREA MURPHYI* (COX, 1864) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Ngairea dorrigoensis												
Dorrigo												
AMC63517 (Holotype)	1	4 1/2-	3.45	6.23	0.55	0.50	1.93	0.26	---	---	0.43	14.4
AMC 63513	1	4 1/8	3.36	5.71	0.59	0.67	2.10	0.32	---	---	0.51	11.20
AMC 142476	1	4 1/2	3.70	6.30	0.59	0.50	1.93	0.26	---	---	0.68	9.26
New England N.P. AMC 142440	1	4 1/2	3.61	5.97	0.60	0.50	1.93	0.26	---	---	0.47	12.7
Tabulam AMC 137757	1	4 7/8-	4.45	6.97	0.64	0.84	2.18	0.39	---	---	0.55	12.6
Beaury S.F.												
OMMO 10939	1	5	4.03	7.31	0.55	0.59	2.02	0.29	---	---	---	---
AMC 142475	1	4 5/8	3.78	6.39	0.59	0.59	2.10	0.28	---	---	0.51	12.5
Acacia Plateau AMC 128560	1	5 1/8	4.37	7.14	0.61	0.92	2.35	0.39	---	---	0.43	16.6
Upper Pine Ck QMMO 16544	3	4 7/8+	3.98±0.323 (3.61–4.62)	7.06±0.196 (6.72–7.40)	0.56±0.031 (0.52–0.62)	0.67±0.098 (0.50–0.84)	2.13±0.102 (1.93–2.27)	0.31±0.032 (0.26–0.37)	---	---	---	---
Canungra AMC 32997	3	4 3/4- (4 1/2+ to4 7/8)	3.53±0.170 (3.36–3.87)	6.10±0.223 (5.88–6.55)	0.580±0.007 (0.57–0.59)	0.560±0.074 (0.42–0.67)	2.190±0.129 (2.02–2.44)	0.260±0.046 (0.17–0.32)	---	---	0.33±0.013 (0.30-0.34)	18.80±1.513 (17.29–21.83)
Running Ck QMMO 16472	1	4 7/8	3.70	6.22	0.59	0.59	2.02	0.29	---	---	---	---
Lamington N.P. QMMO 16448	1	4 7/8-	3.53	6.23	0.57	0.59	2.02	0.29	---	---	---	---
Ngairea levicostata												
Koreelah S.F. QMMO 10959 (Holotype)	1	4 5/8	4.79	6.30	0.76	1.01	2.27	0.44	---	---	0.47	13.35
Cunningham's Gap QMMO 17153	1	4 1/4-	3.95	5.63	0.70	0.67	1.85	0.36		---	0.45	12.46
Ngairea murphyi												
Mt Keira AMC 142962 (Neotype)	1	5 7/8	3.70	5.88	0.63	1.09	1.68	0.65	---	---	1.41	4.19
AMC 150091	1	5	3.19	5.46	0.58	0.67	1.60	0.42	---	---	1.28	4.27
Mt Cambewarra AMC 142968	1	5 1/2	3.19	6.05	0.53	0.58	1.60	0.37	---	---	1.58	3.84
Fitzroy Falls QMMO 16932	1	5 3/8-	2.86	5.80	0.49	0.50	1.60	0.32	---	---	1.32	4.39

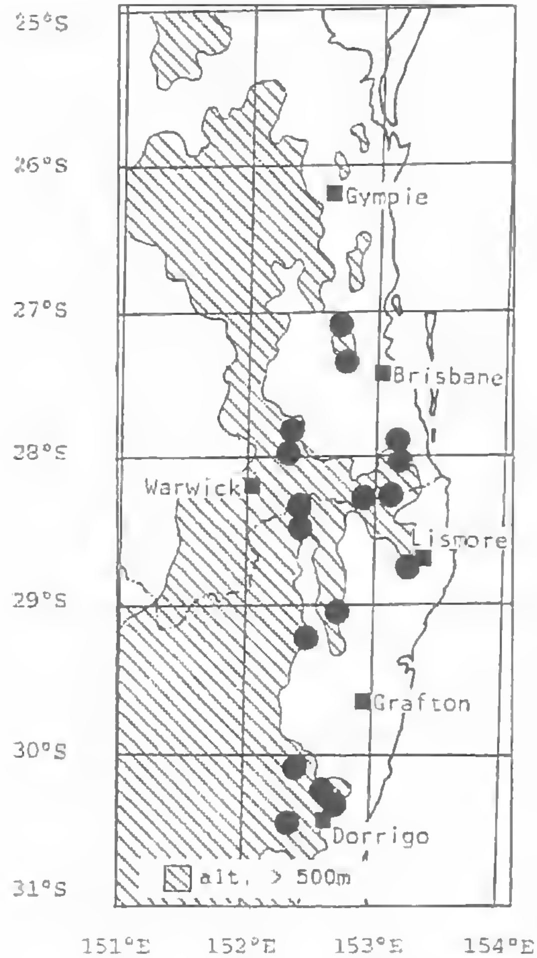


FIG. 5. Distribution of *Ngairea dorrigoensis* (Iredale, 1941).

QMMO16472, 1 Jan 1980, V. Kessner): Upper Pine Creek, Canungra, NVF/*Araucaria*, under bark (15, QMMO16544, 1 Oct 1986, J. Stanisic, D. Potter; 3, QMMO16583, 29 Sept 1986, J. Stanisic, J. Chaseling).

DIAGNOSIS

Shell depressed, large, diameter 5.71–7.40 mm (mean 6.50 mm), with 4 1/8 to 5 1/8 (mean 4 1/4-) normally coiled whorls. Apex and spire moderately elevated, height of shell 3.36–4.62 mm (mean 3.78 mm). H/D ratio 0.52–0.64 (mean 0.58). Body whorl descending slightly in front. SP/BWW 0.17–0.39 (mean 0.31). Protoconch with 1 5/8- to 1 3/4+ whorls, mean diameter 1065.0µm at 1 1/2 whorls. Apical sculpture of low curved radial ribs, without spiral elements (Fig. 3d). Post nuclear sculpture of numerous protractively sinuated radial ribs whose interstices are 5–7 times their width. Microsculpture of crowded raised spiral cords (Fig. 3e). Sculpture continuous on the base (Fig. 3b). Umbilicus small, diameter 0.30–0.68 mm, (mean 0.46 mm), D/U ratio 9.26–21.83 (mean 14.59), to closed. Sutures slightly impressed. Whorls flattened above and below an angulate periphery (Fig. 3c). Body whorl keeled, more angulate in juvenile specimens. Aperture ovately lunate. Lip simple, becoming thickened at the basal margin. Columella thickened and reflected over the umbilicus. Parietal callus white with brown flammulations, pustulose. Colour yellow-horn with reddish-brown flammulations above, continued below the periphery and onto the base in juvenile specimens, but fading toward the umbilicus in adult specimens. Based on 16 measured adults.

Epiphallus internally with longitudinal pilasters, entering penis through a large muscularised pilaster (Fig. 4b). Penis (Fig. 4b) a short cylindrical muscularised tube, more swollen apically; internally with apical muscular collar consisting of 5-6 pad-like thickenings, and slender longitudinal fleshy pilasters in the lower regions. Penial retractor muscle a shortened tuft inserting on the epiphallus near its junction with the penis. Free oviduct muscular reflexed, much longer than vagina (Fig. 4a).

Radula (Fig. 3f) with central tooth having a large, broadly triangular mesocone and reduced ectocones.

Based on six dissected specimens (QMMO6304, QMMO16471, QMMO16470, AMC137757, AMC142476).

RANGE AND HABITAT

Under the bark of rotting logs in moist subtropical notophyll vine forests of cool wet highland areas of the Great Dividing Range (from New England, NSW to the Mistake Mountains, SEQ); the Border Ranges, and the D'Aguilar Range, SEQ: penetrating adjacent drier subtropical forest (low microphyll vine forest, semi-evergreen vine thicket) in the Koreelah Creek and Richmond Range areas, northern NSW.

REMARKS

Northern representatives of *N. dorrigoensis* are larger than their southern counterparts and have the umbilicus more closed (Table 3). Possibly the warmer climate provides a longer growth period in northern populations.

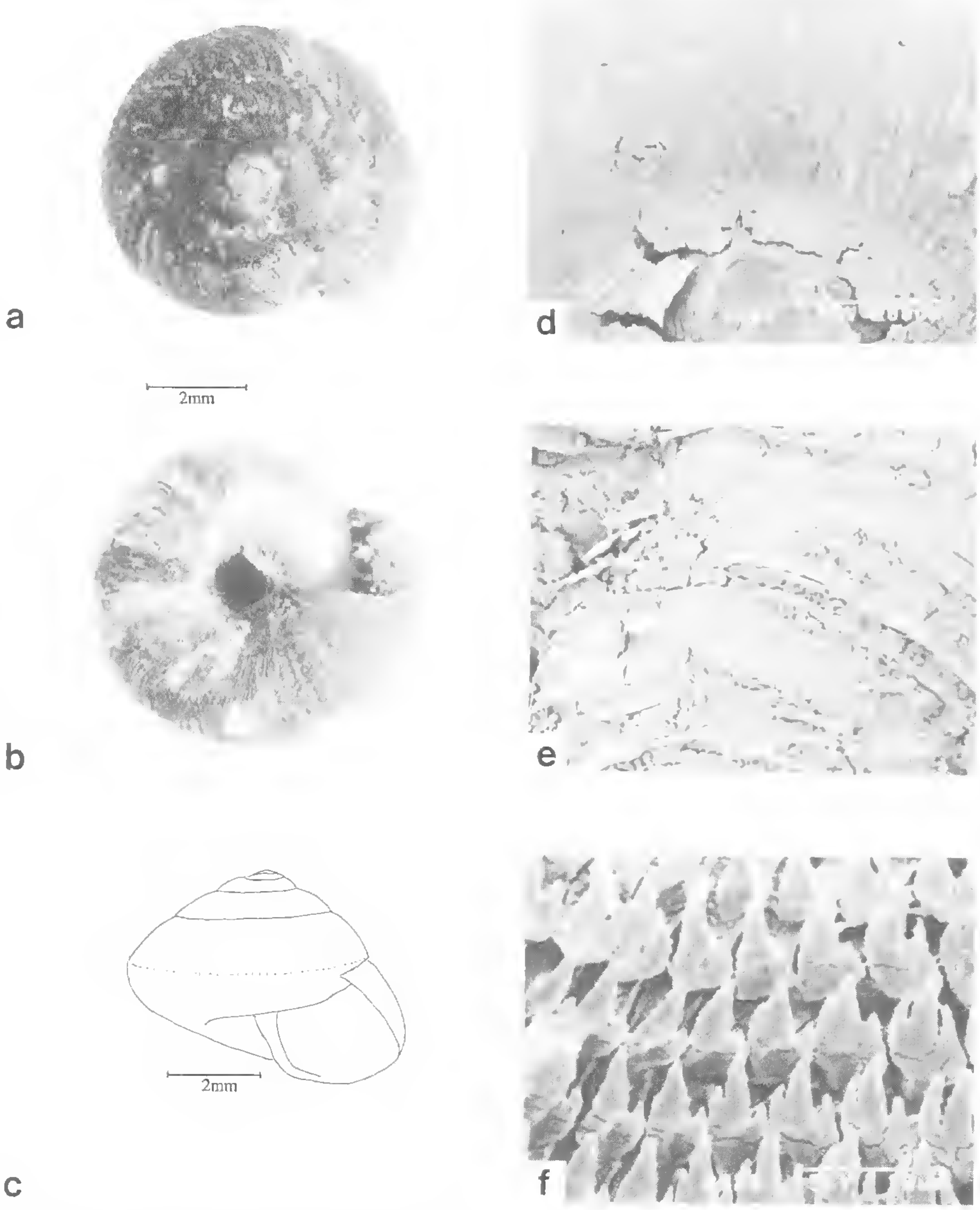


FIG. 6. *Ngairea levicostata* sp. nov. a–c, Along Acacia Plateau Rd, Koreelah S.F., NSW. QMMO10959, holotype; d–f, Cunningham's Gap, SEQ. QMMO17153, QMMO12684, paratypes. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, lateral teeth. Scale lines as marked.

Ngairea levicostata sp. nov.
(Figs 6–8; Tables 2, 3)

ETYMOLOGY

Latin *levis*, smooth; *costa*, rib; referring to reduced microsculpture on major ribs of adult whorls.

COMPARISONS

N. levicostata is most similar to *N. dorrigoensis* but differs in having a higher spire, fewer whorls with different sculptural features, a protoconch with curved radial ridges and fine, weak, crowded spiral cords and in lacking the microsculpture of crowded wavy spiral cords present in *N. dorrigoensis*. Species of *Mussonula* spp. are separable from *N. levicostata* by their exsert protoconchs and apical sculpture of bold spiral cords (Figs 18d, 20f).

TYPE MATERIAL

HOLOTYPE: QMMO10959, Koreelah S.F., NENSW, along Acacia Plateau Rd, 850 m (28°21'S, 152°24'E), 15 Mar 1981, AM/QM - ABRS 1981. Height of shell 4.79 mm, diameter 6.03 mm. H/D ratio 0.76, D/U ratio 13.35, whorls 4 5/8.

PARATYPES: Cunninghams Gap, SEQ, near top, 755 m, NVF/*Araucaria* (28°04'S, 152°24'E) (3, QMMO12684, QMMO10994, AMC128610, 16 Mar 1981, AM/QM - ABRS 1981); Cunningham's Gap, SEQ, leaf litter (1, QMMO17153, 18 Jun 1979, G. Annabell).

DIAGNOSIS

Shell trochoid, large, diameter 5.63–6.30 mm (mean 5.97 mm) with 4 1/4 to 4 5/8 (mean 4 1/2-) loosely coiled whorls. Apex and spire strongly elevated, height of shell 3.95–4.79 mm (mean 4.37 mm), H/D ratio 0.70–0.76 (mean 0.73). Body whorl descending more rapidly, SP/BWW ratio 0.36–0.44 (mean 0.40). Protoconch with 1 5/8 whorls, mean diameter 1119.0μm at 1 1/2 whorls. Apical sculpture of low curved radial ribs crossed by raised spiral cords (Fig. 6d). Post nuclear sculpture of numerous crowded, high, protractively sinuated radial ribs (Fig. 6e). Fine raised microspiral lines present but no microriblets. Sculpture continued onto the base (Fig. 6b). Umbilicus narrow U-shaped, diameter 0.45–0.47 mm (mean 0.46 mm), D/U ratio 12.46–13.35, (mean 12.91). Sutures impressed. Whorls flattened above and rounded below an angulate periphery (Fig. 6c). Aperture subquadrate. Lip simple with a slight thickening at the baso-columellar margin. Columella almost vertical, reflected toward the umbilicus. Parietal callus well developed. Colour yellow-horn with adhering dirt particles. Based on 2 measured adults.

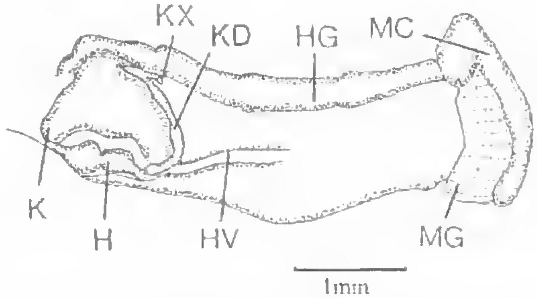


FIG. 7. *Ngairea levicostata* sp. nov. Cunningham's Gap, SEQ. QMMO12684, paratype. Pallial cavity. Scale line as marked.

Foot and tail moderately broad, tapering posteriorly with a weak caudal horn. Mantle collar thickened with a strongly developed glandular zone (Fig. 7). Kidney vaguely triangular c. 1/3 length of pallial cavity, rectal lobe reduced. Pulmonary vein inconspicuous. Reproductive system immature.

Radula (Fig. 6f) with central tooth having a slender lanceolate mesocone and small but prominent side cusps; inner laterals with slender mesocone, endocone absent and weakly developed ectocone.

Based on one dissected specimen (QMMO12684).

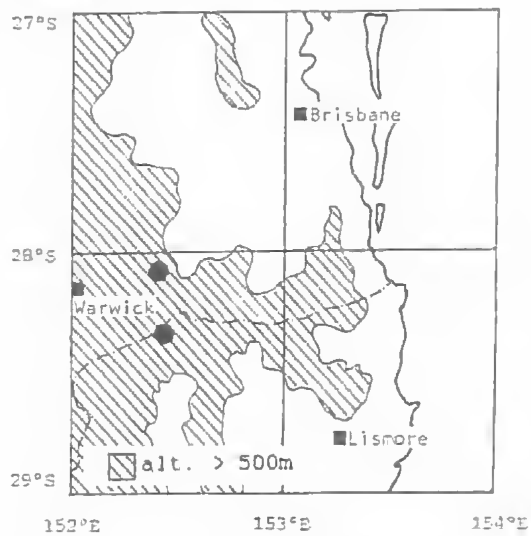
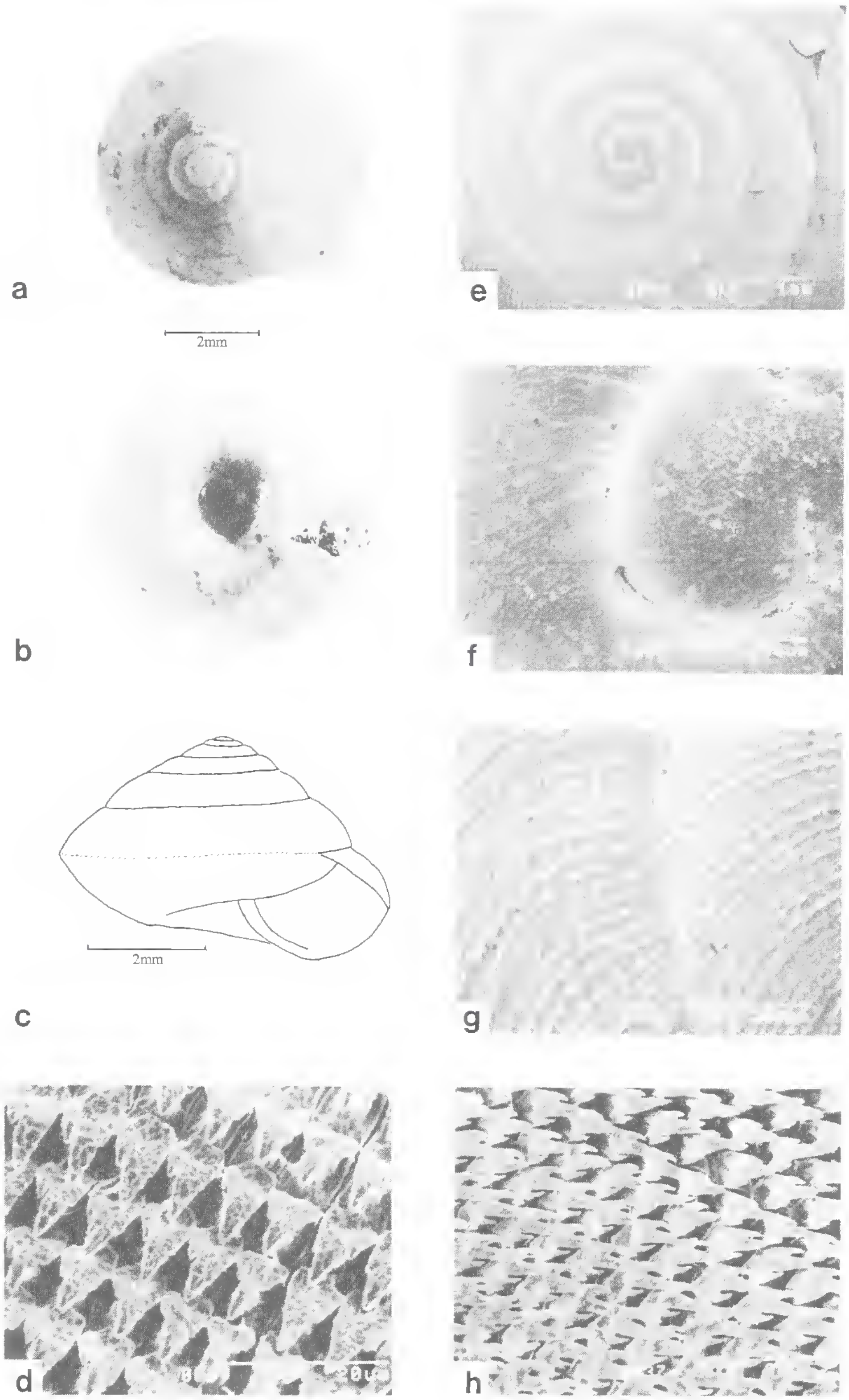


FIG. 8. Distribution of *Ngairea levicostata* sp. nov.


a
2mm
b
2mm
c
d
e
f
g
h

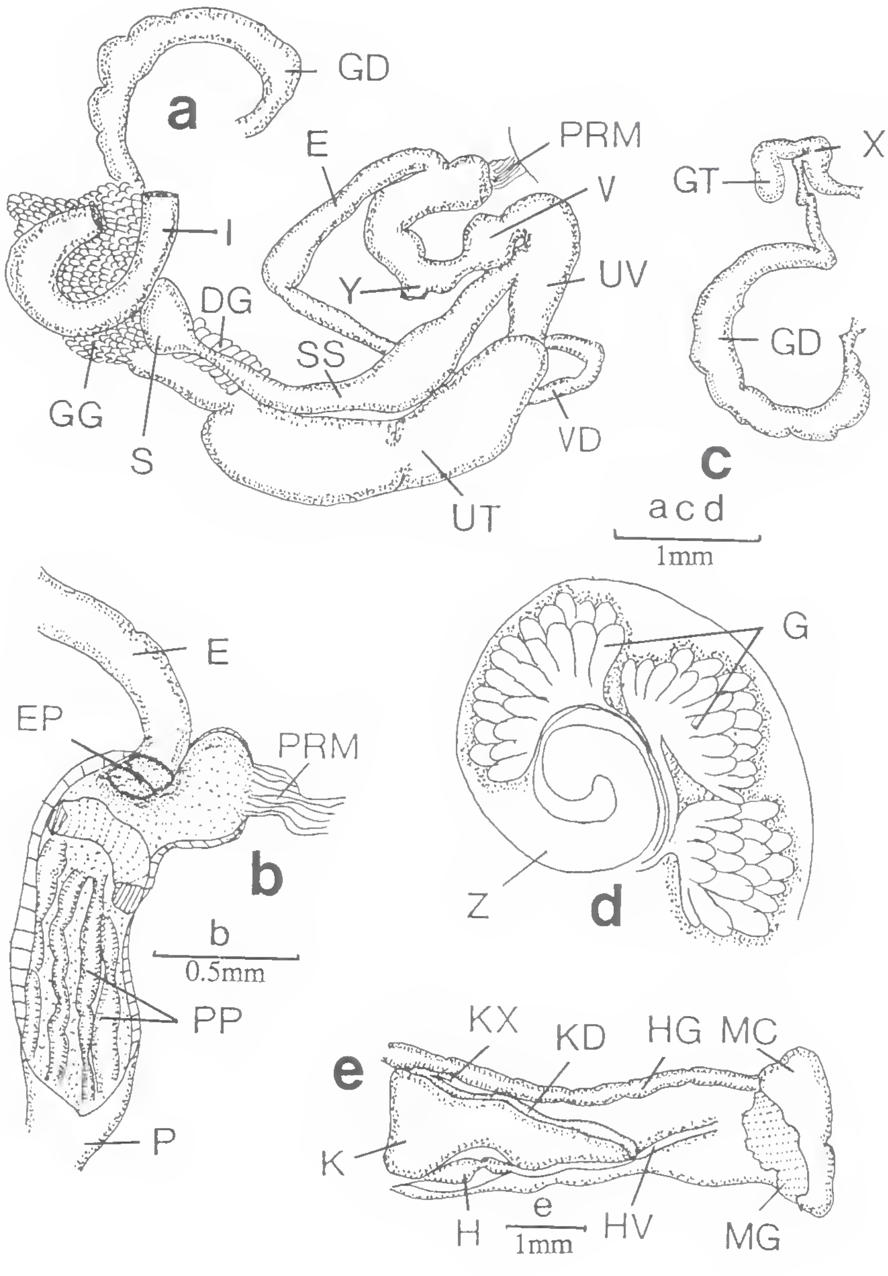


FIG. 10. *Ngairea murphyi* (Cox, 1864). c. 4km E of Fitzroy Falls on Kangaroo Valley - Fitzroy Falls Rd, NSW. QMMO16932. a, genitalia; b, details of penis interior; c, talon and hermaphroditic duct; d, ovotestis; e, pallial cavity. Scale lines as marked.

FIG. 9. *Ngairea murphyi* (Cox, 1864). a–c, Mt Keira, Wollongong, NSW. AMC142962, neotype; e-g, Woodhill NSW, AMC142968; d,h, c. 4km E of Fitzroy Falls on Kangaroo Valley-Fitzroy Falls Rd, NSW. QMMO16932. a–c, entire shell; d, central and lateral teeth; e, spire; f, apical sculpture; g, post nuclear sculpture; h, lateromarginal teeth. Scale lines as marked.

RANGE AND HABITAT

N. levicostata is known from two localities on the cool wet highlands of the Great Dividing Range in northern NSW and SEQ where it is sympatric with *N. dorrigoensis*. The microhabitat is unknown.

REMARKS

N. levicostata is erected to assist comparative and biogeographical discussions; its conchological features are distinctive. Although the general shell facies relates to *Mussonula*, *N. levicostata* is included in *Ngairea* primarily on form of the protoconch.

Ngairea murphyi (Cox, 1864) comb. nov.
(Figs 9–11; Tables 2, 3)

Helix murphyi Cox, 1864, p. 37; Cox, 1868, p.23.
Paralaoma murphyi (Cox); Iredale, 1937a, p. 314; Iredale, 1941a, p. 264.

COMPARISONS

N. murphyi is a southern outlier distinguished within the genus by its higher whorl count and wider umbilicus (Table 2). *N. dorrigoensis* which it most resembles, has a tiny to closed umbilicus, weaker keel, fewer whorls and protoconch with curved radial ridges (Fig. 3d). Apical sculpture involves irregular radial rugosities and spiral wrinkles producing a pitted effect (Fig. 9f). Anatomically distinctive are the penis with epiphallic pore located subapically and the penial retractor muscle inserted apically (Fig. 10b).

PREVIOUS STUDIES

Cox (1864) introduced the name without an accompanying figure and referred to it again without figures in 1868. A further listing (Cox, 1909, p. 54) was accompanied by an explanation for the lack of figures: "I fear the types of this species have disappeared from our (Australian) Museum Collection. The specimens of it which I possessed were unfortunately smashed while in the artists hands". The large whorl count, small size, widely open umbilicus, sharply keeled body whorl and reticulate sculpture, referred to in Cox's original description, together with the type locality of Wollongong, NSW, effectively fix Cox's name to the species discussed below. The neotype was collected at Mt Keira, Wollongong, which I consider to be near the original type locality.

Iredale (1937a, p. 314) placed *H. murphyi* in *Paralaoma* Iredale, 1913, without explanation, later (Iredale, 1941a, p. 264) admitting that no known specimens of *H. murphyi* existed and that this decision was based on broad details of Cox's description. In *Paralaoma* the shell is much smaller, more fragile, with fewer whorls and bold spiral cords on the protoconch. Although morphology of *N. murphyi* is unusual, penial morphology, shell sculpture and peculiar body colour are considered sufficient to endorse the new generic placement.

TYPE MATERIAL

NEOTYPE: AMC142962, Mt Keira, Wollongong, NSW, Collected by C.F. McLauchlan, 6 Nov 1948. Height of shell 3.70 mm, diameter 5.88 mm, H/D ratio 0.63, D/U ratio 4.19, whorls 5 7/8.

OTHER MATERIAL

c. 4 km E of Fitzroy Falls on Kangaroo Valley - Fitzroy Falls road, NSW, temperate rainforest, under bark of fallen tree (5, QMMO16932, J. Stanisic, 4 Jan 1987); Woodhill, c. 4 mls NW of Berry, NSW, mixed forest, E side of range (1, AMC142968, W. Ponder, 14 Nov 1970); Mt Cambewarra, nr Nowra, NSW (1 AMC142964, L. Price, 30 Oct, 1963); Mt Keira, Wollongong, NSW, from rainforest at scout camp (1, AMC142962, C.F. McLauchlan, 6 Nov 1948).

DIAGNOSIS

Shell depressed to elevated trochoid, moderately large, diameter 5.46–6.05 mm (mean 5.80

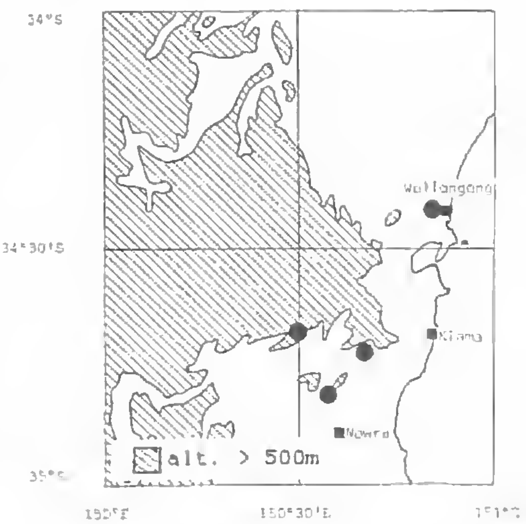


FIG. 11. Distribution of *Ngairea murphyi* (Cox, 1864) in the Illawarra region, New South Wales.

mm) with 5 to 5 7/8 (mean 5 1/2-) tightly coiled whorls. Apex and spire weakly to strongly elevated, height of shell 2.86–3.70 mm (mean 3.24 mm), H/D ratio 0.49–0.63, (mean 0.56). Body whorl not descending in front, SP/BWW 0.32–0.65 (mean 0.44). Protoconch with irregular curved radial ridges and pits, spiral elements absent (Fig. 9f). Post nuclear sculpture of numerous, crowded, protractively sinuated radial ribs (Fig. 9e, g), whose interstices are about 5–7 times their width. No microriblets. Microsculpture of numerous, crowded, narrow spiral cords. Sculpture continuous on the base but reduced (Fig. 9b). Umbilicus relatively wide, V-shaped, diameter 1.28–1.58 mm (mean 1.39 mm), D/U ratio 3.84–4.39 (mean 4.17). Sutures impressed. Whorls flattened above and below a carinate periphery (Fig. 9c). Aperture ovately lunate to subquadrate. Lip simple with a slight thickening at the baso-columellar margin. Columella almost vertical, slightly reflected toward the umbilicus. Parietal callus well developed, white, pustulose. Colour creamy-yellow horn without flammulations. Based on four measured adults.

Kidney (Fig. 10e) with elongate pericardial lobe and no rectal lobe, 1/2 length of the pallial region. Ovotestis (Fig. 10d) three or more clumps of creamy-white palmately clavate lobes of alveoli. Epiphallus (Fig. 10a) twice length of the penis with internal longitudinal pilasters, entering penis subapically through a muscular pilaster (Fig. 10b). Penis (Fig. 10b) short, cylindrical, muscularised, internally with an apical muscular collar and fleshy, longitudinal pilasters below the collar. Penial retractor muscle (Fig. 10a, b) inserted apically on the penis. Vagina relatively long (Fig. 10a).

Radula (Fig. 9d, h) with mesocone of central tooth slender lanceolate and ectocones small but prominent.

Based on 2 dissected specimens (QMMO19632).

RANGE AND HABITAT

N. murphyi occurs in an area which has been greatly altered and disturbed by white settlement (Baur, 1957, pp. 191, 195). Its distribution encompasses the remnant patches of moist warm temperate and cool subtropical vine forests of the Illawarra region, NSW, from Wollongong south to Mt Cambewarra, near Nowra. The original specimens were taken from under stones; live material has been collected from under bark of a fallen tree (QMMO16932).

REMARKS

The high whorl count has not been observed in any other east coast charopid with a trochoid shell. The North Queensland helicarionid *Theskelomensor* Iredale, 1933 has a trochoid shell, wide umbilicus and high whorl count but the similarity is convergent. The few available specimens of *N. murphyi* show a great deal of variation in shell height brought about by changes in spire protrusion (Table 3).

Ngairea canaliculata sp. nov.
(Figs 12–14; Tables 2, 4)

Flammulina corticicola (Cox): Hedley, 1912 (part), p. 264, but not figures.

ETYMOLOGY

Latin *canaliculus*, small channel; for the channelled sutures.

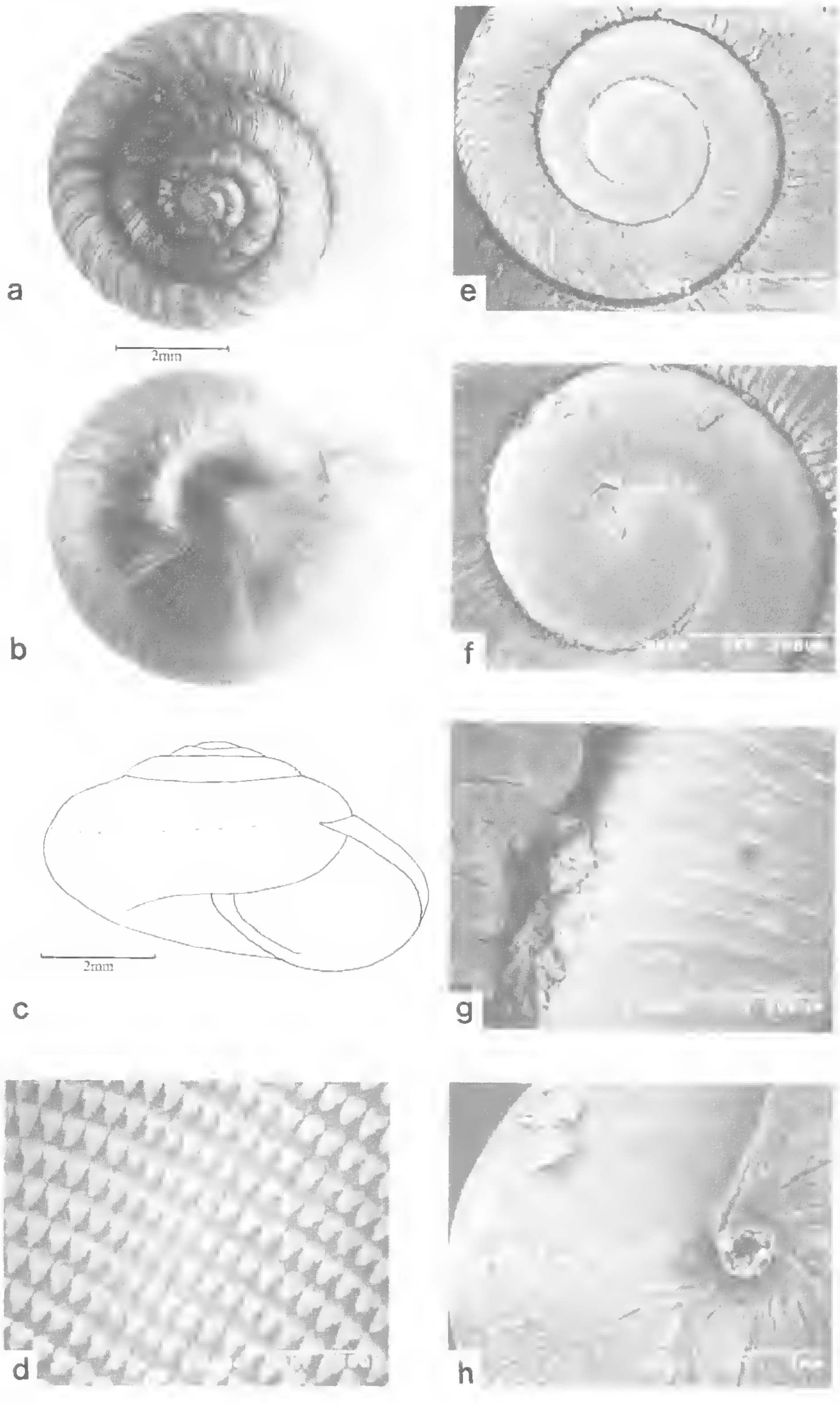
COMPARISONS

Readily identified by its channelled sutures, low spire, rounded periphery and sculpture of low, broad radial ridges crossed by fine, crowded microspiral grooves (Fig. 12g). *Lenwebbia protoscrobiculata* which is sympatric with *N. canaliculata* has similar shell shape but differs markedly by having a punctate protoconch, fine thread-like radial riblets on the body whorl, and simple sutures (Fig. 29c–g).

TYPE MATERIAL

HOLOTYPE: QMMO16454, Beauty Spot 98, Kroombit Tops, SEQ. Collected by G.B. Monteith, 29 Sept 1983. Height 3.87 mm, diameter 6.55 mm, H/D ratio 0.59, whorls 4 5/8.

PARATYPES: SOUTH EAST QUEENSLAND - QMMO17154, 1 specimen, same data as holotype; Kroombit Tops, TA 47 creek (1, QMMO16467, 9-19 Dec. 1983, G.B. Monteith, G. Thompson); Kroombit Tops, under palm fronds, NVF/Palms (1, QMMO14890, 8 May 1984, J. Stanisic, D. Potter); Mt Fort William, Kalpowar S.F., NVF (24°39'S, 151°20'E) (2, QMMO12598, AMC136757, 4 Sept 1982, ABRS - AM/QM; Camp Creek, S of Miriam Vale, SW side of Bobby Range, MVF (24°36'20"S, 151°33'E) (3, QMMO13290, AMC137913, 6 Sept 1982, ABRS - AM/QM); Rainforest walk, Kalpowar S.F., MVF/*Araucaria*, (24°41'S, 151°21'E) (4, AMC-136742, QMMO12574, 4 Sept 1982, ABRS - AM/QM); Bobby Range S.F., NVF (24°37'S, 151°32'E) (2, QMMO12151, AMC136509, 6 Sept 1982, ABRS - AM/QM); Bulburin (Austral) S.F., S of Gladstone, 580 m (24°34'S, 151°29'E) (1,


a
2mm
b
2mm
c
d
e
f
g
h

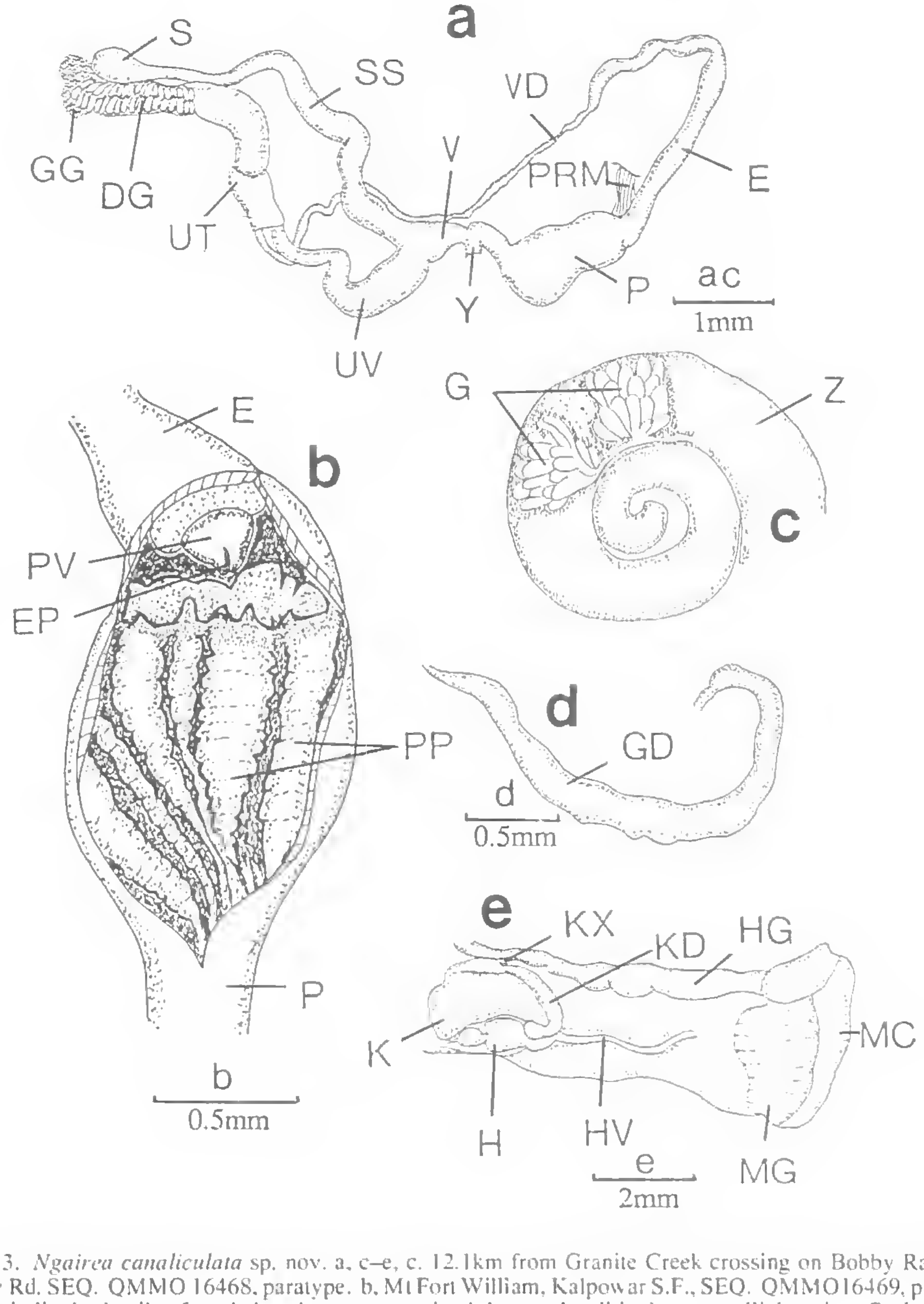


FIG. 13. *Ngairea canaliculata* sp. nov. a, c–e, c. 12.1km from Granite Creek crossing on Bobby Range-Mt Perry Rd. SEQ. QMMO 16468, paratype. b, Mt Fort William, Kalpowar S.F., SEQ. QMMO16469, paratype. a, genitalia; b, details of penis interior; c, ovotestis; d, hermaphroditic duct; e, pallial cavity. Scale lines as marked.

FIG. 12. *Ngairea canaliculata* sp. nov. a–c. Beauty Spot 98. Kroombit Tops, SEQ. QMMO16454, holotype; d–h, summit, Mt Fort William, Kalpowar S.F., SEQ. QMMO16469, paratype. a–c, entire shell; d, central and lateral teeth; e, details of spire showing channelled sutures; f, apical sculpture; g, post nuclear sculpture; h, details of base and umbilicus. Scale lines as marked.

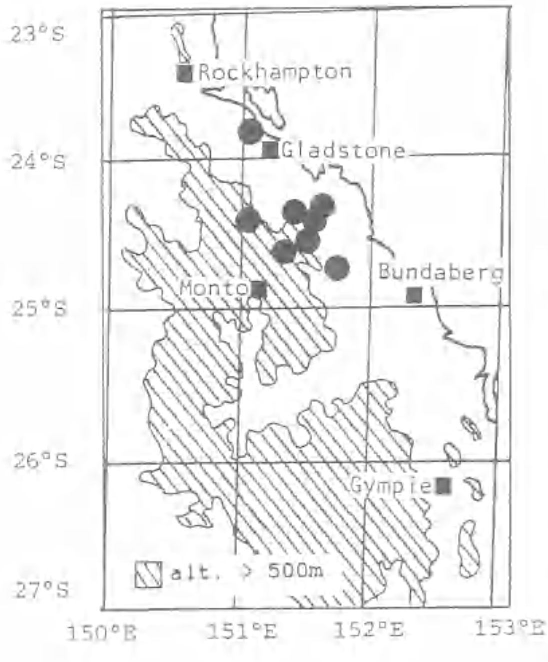


FIG. 14. Distribution of *Ngairea canaliculata* sp. nov.

AMC142465, 8 May 1975, J.B. Burch, W.F. Ponder, P.H. Colman); Bulburin (Austral) S.F., S of Gladstone, 540 m, CNVF-A1 forest type (24°31'S, 151°29'E) (1, AMC142466, J.B. Burch, W.F. Ponder, P.H. Colman); Bottle-tree scrub, west of Gladstone, on the ground under leaves (1, AMC32998, Aug 1908, S.W. Jackson); Colosseum Creek, 16 km S of Miriam Vale (2, AMC142445, 25 May 1958, L. Price); Kalpowar S.F., litter, MVF/Araucaria (9, QMMO16459, 4 Jul 1984, D. Potter, J. Stanisic, K. Emberton); Mt Larcom, on rocky slope, litter, SEVT (2, QMMO16443, 9 May 1984, J. Stanisic, D. Potter); Summit, Mt Fort William, Kalpowar S.F., under bark, CNVF (4, QMMO16469, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton); c. 12.1 km from Granite Creek crossing on Bobby Range - Mt Perry Road, under bark of fallen trees, NVF/Palms (24, QMMO16468, 16 Sept 1985, J. Stanisic, D. Potter).

OTHER MATERIAL

SOUTH EAST QUEENSLAND: Colosseum Creek, SW of Miriam Vale, rainforest along creek (24°23'30"S, 151°27'E) (2, AMC137890, QMMO13223, 6 Sept 1982, ABRS - AM/QM); Summit of Mt Booroon Booroon, on rocky slope, litter, MVF/*Araucaria* (2, QMMO16444, 17 Sept 1985, J. Stanisic, D. Potter); Kroombit Tops, 13 km W of 'Chapman's', NVF (24°25'S, 151°02'E) (1, QMMO12222, 6 Sept 1982, ABRS - AM/QM); Port Curtis (3, AMC63752, ex Cox); near Colosseum Ck, 16 km S of Miriam Vale (4, AMC142446, 24 May 1958, L. Price); Miriam Vale (1, AMC152447, ex Musson).

DIAGNOSIS

Shell depressed, moderately large, 5.97–7.39 mm (mean 6.53 mm) in diameter, with 4 1/2 to 4 3/4 (mean 4 5/8-) normally coiled whorls. Apex and spire moderately elevated, height of shell 3.28-5.35 mm (mean 3.83 mm). H/D ratio 0.53-0.83 (mean 0.59). Body whorl descending only slightly in front, SP/BWW ratio 0.18–0.32 (mean 0.24). Protoconch flat, shiny, with 1 5/8 to 1 5/8+ whorls, mean diameter 1169.0μm at 1 1/2 whorls. Apical sculpture of very weak, low, curved radial ridges crossed by irregularly spaced incised spiral lines (Fig. 12f). Post nuclear sculpture of numerous, regularly spaced, low, broad, protractively sinuated radial ribs (Fig. 12e), whose interstices are about 7–9 times their width. No intervening microriblets. Microsculpture of incised spiral lines (Fig. 12g). Sculpture continuing onto base (Fig. 12h) with spirals fading toward the umbilicus. Umbilicus small, diameter 0.43–0.94 mm (mean 0.71), D/U ratio 7.21–15.63 (mean 9.40). Sutures distinctly channelled. Whorls rounded above and below the periphery (Fig. 12c). Body whorl without any noticeable angulation, even in juvenile specimens. Aperture ovately lunate. Lip simple, becoming thickened at the baso-columellar margin. Columella thickened, twisted and slightly reflected over the umbilicus. Parietal callus pustulose with some flammulations. Colour deep golden-horn with regularly arranged reddish-brown flammulations above, continuing below the periphery but fading near the umbilicus. Based on 21 measured specimens.

Vas deferens (Fig. 13a) a very thin tube delicately convoluted along its length. Epiphallus (Fig. 13a) very long, muscularised, reflexed half way along its length, internally with longitudinal pilasters, entering penis apically (Fig. 13b) through a conical verge (Fig. 13b). Penial retractor muscle long, inserted at the epiphallus-penis junction. Penis (Fig. 13b) a cylindrical, muscularised tube, swollen apically, internally with an apical fleshy collar and low, corrugated, spongy longitudinal pilasters. Free oviduct (Fig. 13a) strongly muscularised, about 3–4 times the length of the vagina. Vagina very short, internally with fleshy longitudinal lamellae. Atrium short, without unusual features.

Central tooth of radula (Fig. 12d) with broad triangular mesocone and small ectocones.

Based on 6 dissected specimens (QMMO14890, QMMO16468, QMMO16469).

RANGE AND HABITAT

Ngairea canaliculata inhabits warm moist subtropical notophyll vine forests of the ranges and mountain caps between Colosseum Creek and Mt Larcom, SEQ. This region also has large areas of drier sub-tropical forest (vine thickets and microphyll vine forests) but *N. canaliculata* shows little tendency to occur outside of the moister areas. The species has been collected live under bark and in the rolled up stems of discarded palm fronds.

REMARKS

This species was first collected by Sidney W. Jackson in 1908, but included under *Flammulina corticicola* (Cox, 1866) by Hedley (1912). It is distinguishable from that species by its channelled sutures and radially sculptured base. The channelled suture is an unusual development seen in a limited number of Australian, New Zealand and Pacific Island species.

Ngairea corticicola (Cox, 1866) comb. nov.
(Figs 15–17; Tables 2, 4)

Helix corticicola Cox, 1866a, p. 374 ;Cox, 1868, p. 19, pl.7, figs 7–7a.

Oreokera corticicola (Cox); Iredale, 1937a, p.318; Iredale, 1941a, p. 264.

COMPARISONS

N. corticicola can be distinguished from *N. dorrigoensis* by its less prominent radial sculpture, almost smooth base, more rounded periphery, microsculpture of incised spiral grooves (Fig. 15f) and penis with corrugated, longitudinal pilasters and a continuous, weakly muscular, apical collar. *N. canaliculata* (Fig. 12) has similar microsculpture to *N. corticicola* but differs in having low broad radial ridges, fewer whorls, less elevated spire, channelled sutures, more rounded shell periphery and an epiphallus almost twice as long as the penis (Fig. 16a).

PREVIOUS STUDIES

Hedley (1912) attempted to clarify *Helix corticicola* Cox, 1866 but he considered specimens from Canungra, SEQ, to be conspecific and figured a representative. This was the species later described by Iredale (1941a) as *Oreokera dorrigoensis*. *N. corticicola* occurs microsympatrically with *N. dorrigoensis* at Pine Creek, Canungra, but the two species can be distinguished by sculpture on the base of shell, which is reduced in the former and strongly radial in the latter.

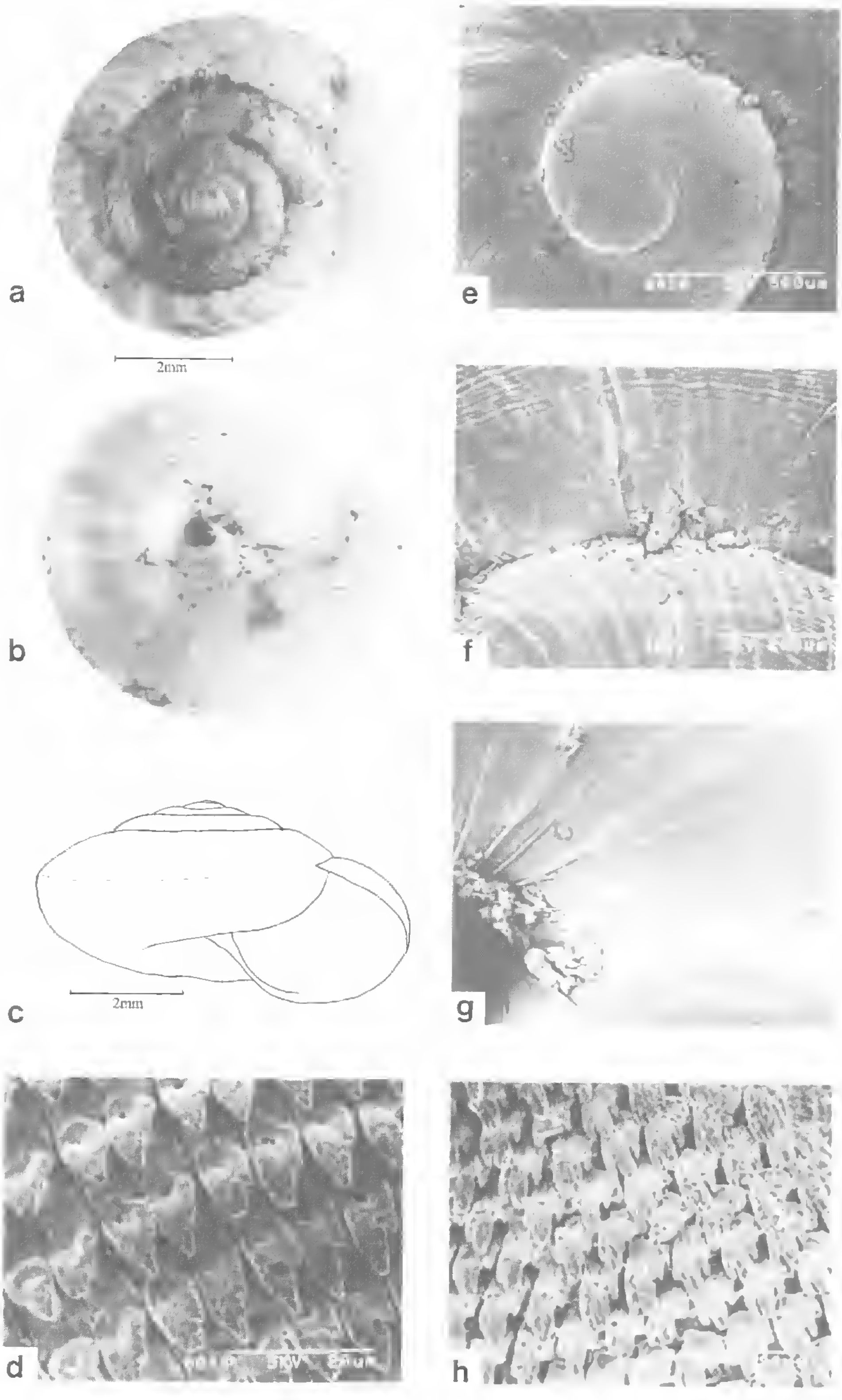
TYPE MATERIAL

LECTOTYPE: AMC63520, Lismore, NSW, Cox collection. Height of shell 3.87 mm, diameter 6.47 mm, H/D ratio 0.60, D/U ratio 10.78, whorls 5.

PARALECTOTYPES: AMC63511, 3 specimens, same data as lectotype.

OTHER MATERIAL

NEW SOUTH WALES: Wollongbar (1, AMC142431, Aug 1905); Richmond River (4, AMC142432, ex Cox, Petterd); Rous Mill, Richmond Rv., (6, AMC142433, 1900, S.W. Jackson); Lismore, Richmond Rv., (9, AMC142434, ex Brazier); Richmond Rv., (1, AMC142435, ex Helms); upper Tweed River (7, AMC142436, ex Cox, Petterd); Lowanna, near Dorrigo (1, AMC63816, M. Ward); Borngall Ck, Bellinger River, under bark (1, AMC142437, ex Cox); opposite Kelly selection, 16 km from Murwillumbah, in gully on main road (3, AMC63835); Red Scrub Flora Reserve, Whian Whian S.F., 210 m (28°38'S, 153°19'E) (13, AMC142473, 15 May 1976, P.H. Colman, I. Loch); Terania Creek, Whian Whian S.F., 340 m, (28°34'S, 153°19'E) (1, AMC142474, 16 May 1976, P.H. Colman, I. Loch); Dorrigo Range, (4, AMC142438, Apr 1957, L. Price); Ballina, in rotten wood (10, AMC142439, ex Cox); Big Scrub, Whian Whian State Forest, litter, SNVF (1, QMMO16441, 15 Nov. 1983, ABRS - AM/QM); Upper Wilson's Creek, litter, NVF (28°32'S, 153°24'E) (1, QMMO16443, 16 Nov 1983, ABRS - AM/QM); Nightcap Range, under bark of fallen tree (28°34'S, 153°20'E) (2, QMMO16466, 15 Nov 1983, ABRS - AM/QM); The Glade, Dorrigo N.P., under log, cool temperate rainforest (30°22'20"S, 152°43'40"E) (1, QMMO14766, 12 Nov 1983, ABRS - AM/QM); Swan's Road, Bruxner Park Flora Reserve, under bark of fallen logs and in palm fronds on ground, subtropical rainforest (22, QMMO14767, QMMO16757, 14 Nov. 1983, ABRS - AM/QM); Woolgoolga Ck Flora Reserve, Wedding Bells S.F., under leaf in subtropical rainforest (1, AMC152252, Mar 1983, M. Shea); Currumbin Valley Nature Reserve, under log in rainforest (3, AMC152254, Jul 1977, M. Shea); Lismore Scrub, Lismore, under bark of fallen trees, remnant rainforest (4, QMMO17135, 9 Mar 1987, J. Stanisic, D. Potter); Wonga Walk, The Glade, Dorrigo N.P., under bark of fallen trees, rainforest (35, QMMO17146, 6 Mar 1987, J. Stanisic, D. Potter); Never Never Picnic Area,


a
2mm
b
c
2mm
d
e
f
g
h

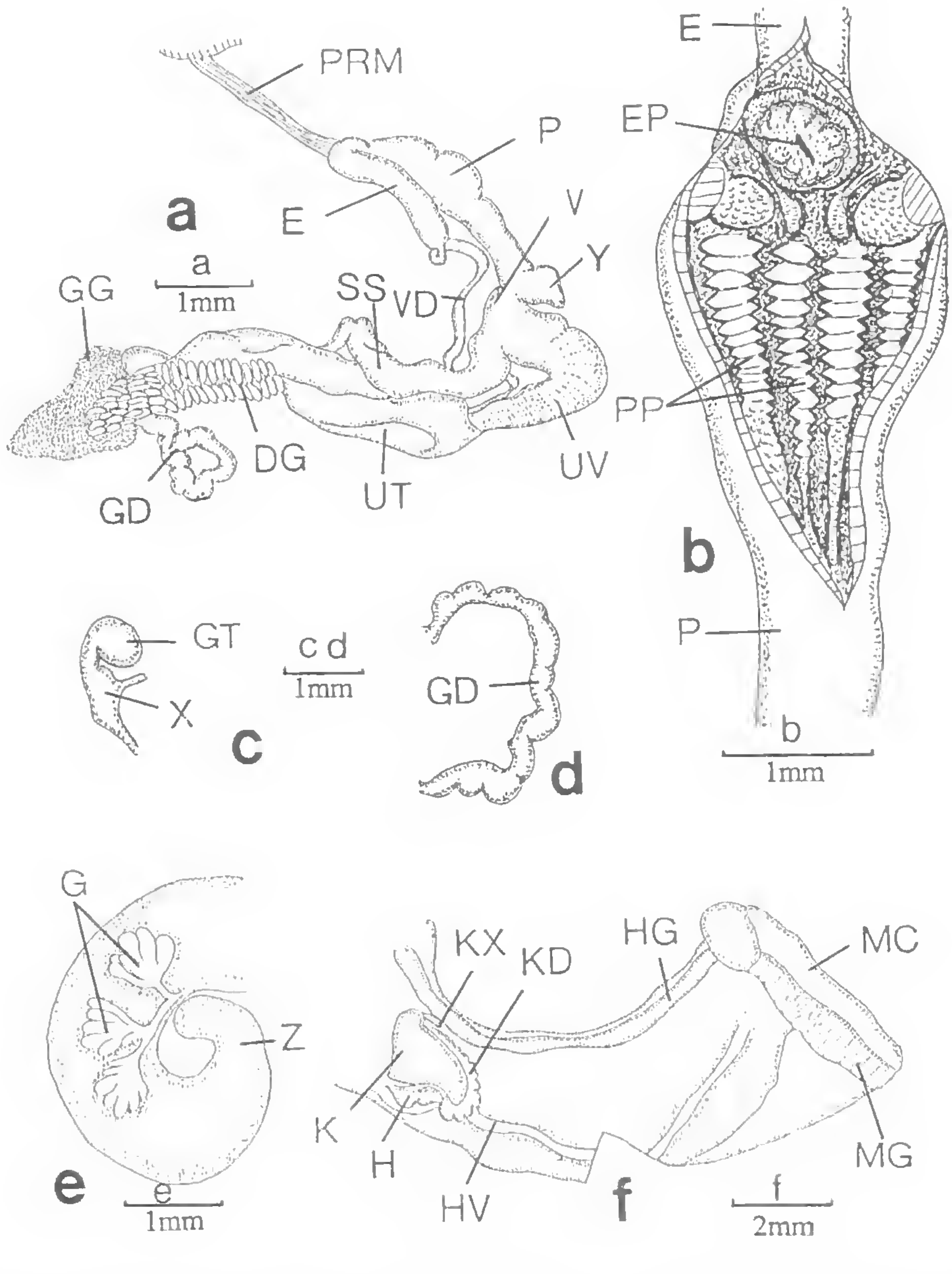


FIG. 16. *Ngairea corticicola* (Cox, 1866). Slopes of Mt Hobwee, Lamington N.P., SEQ. QMMO16462. a, genitalia; b, details of penis interior; c, talon; d, hermaphroditic duct; e, ovotestis; f, pallial cavity. Scale lines as marked.

FIG. 15. *Ngairea corticicola* (Cox, 1866). a-b, Lismore, NSW. AMC63520, holotype; c, Tullawallal Circuit, Lamington N.P., SEQ. QMMO16465; e-g, Red Scrub F.R., Whian Whian S.F., NSW. AMC142473; d, h, Slopes of Mt Hobwee, Lamington N.P., SEQ. a-c, entire shell; d, central (bottom left) and lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, details of umbilicus; h, lateromarginal teeth. Scale lines as marked.

TABLE 4 - LOCAL VARIATION IN *NGAIREA CANALICULATA* SP. NOV. AND *NGAIREA CORTICICOLA* (COX, 1866) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Ngairea canaliculata												
Kroombit Tops												
QMMO 16454 (Holotype)	1	4 5/8	3.87	6.55	0.59	0.67	2.10	0.32	---	---	0.64	10.23
QMMO 17154	1	4 5/8	4.03	6.72	0.60	0.59	2.27	0.26	---	---	0.64	10.50
QMMO 16467	1	4 1/2	4.03	6.72	0.60	0.67	2.27	0.30	---	---	0.43	15.63
Bobby Range												
QMMO 13290	1	4 1/2	3.87	6.97	0.56	0.42	2.27	0.19	---	---	0.64	10.89
QMMO 12151	1	4 5/8	3.53	6.13	0.58	0.50	2.10	0.24	---	---	0.60	10.22
AMC 142465	1	4 1/2-	3.28	5.97	0.55	0.42	2.10	0.20	---	---	0.64	9.33
AMC 142466	1	4 1/2-	3.53	6.47	0.55	0.42	2.10	0.20	---	---	0.60	10.78
Kalpowar S.F.												
QMMO 12574	2	4 1/2	3.45±0.085	6.14±0.165	0.56±0.030	0.46±0.040	2.14±0.015	0.22±0.015	---	---	0.64	9.59±0.255
		(4 1/2–4 1/2+)	(3.36–3.53)	(5.97–6.30)	(0.53–0.59)	(0.42–0.50)	(2.10–2.18)	(0.20–0.23)				(9.33–9.84)
QMMO 12598	1	4 1/2+	3.78	6.55	0.58	0.42	2.10	0.20	---	---	0.72	9.10
AMC 136742	1	4 3/4	4.20	6.89	0.61	0.42	2.02	0.21	---	---	0.94	7.33
QMMO 16459	6	4 5/8+	3.87±0.072	6.58±0.126	0.59±0.012	0.53±0.041	2.17±0.051	0.25±0.014	---	---	0.78±0.018	8.45±0.274
		(4 1/2–4 3/4)	(3.70–4.20)	(6.13–6.97)	(0.55–0.62)	(0.34–0.59)	(1.93–2.27)	(0.18–0.27)	---	---	(0.72–0.85)	(7.21–9.05)
Mt Larcom												
QMMO 16443	1	4 1/2	5.35	6.47	0.83	0.59	2.27	0.26	---	---	0.81	7.99
Colosseum Creek												
AMC 142445	2	4 1/2+	3.45	6.31±0.085	0.55±0.005	0.46±0.040	2.06±0.050	0.23±0.050	---	---	0.75±0.025	8.47±0.170
			(4 1/2–4 5/8+)	(6.22–6.39)	(0.54–0.55)	(0.42–0.50)	(2.02–2.10)	(0.21–0.24)	---	---	(0.72–0.77)	(8.30–8.64)
Ngairea corticicola												
Lismore												
AMC 63520 (Holotype)	1	5	3.87	6.47	0.60	0.67	2.10	0.32	---	---	0.60	10.78
Whian Whian S.F.												
AMC 142473	2	4 3/4	3.78±0.250	6.51±0.460	0.58	0.76±0.085	2.23±0.125	0.34±0.020	---	---	0.79±0.150	8.43±1.020
		(4 1/2–5)	(3.53–4.03)	(6.05–6.97)		(0.67–0.84)	(2.10–2.35)	(0.32–0.36)			(0.64–0.94)	(7.41–9.45)
Bruxner Park												
QMMO 16757	4	4 5/8+	3.81±0.126	6.77±0.228	0.56±0.009	0.69±0.003	2.12±0.020	0.33±0.008	---	---	0.86±0.010	7.88±0.338
		(4 5/8–4 3/4+)	(3.53–4.12)	(6.22–7.31)	(0.54–0.58)	(0.67–0.76)	(2.10–2.18)	(0.32–0.35)			(0.85–0.89)	(6.99–8.60)
Upper Wilsons Ck												
QMMO 16443	1	4 3/4+	4.12	7.23	0.57	0.59	2.02	0.29	---	---	0.94	7.69
Booyong Flora Reserve												
QMMO 17005	2	4 3/4	3.49±0.040	5.93±0.045	0.59	0.68±0.085	2.10±0.080	0.32±0.030	---	---	0.72	8.23±0.060
		(4 3/4–4 3/4+)	(3.45±3.53)	(5.88–5.97)		(0.59–0.76)	(2.02–2.18)	(0.29–0.35)				(8.17–8.29)
Murwillumbah												
AMC 63835	3	5 1/8-	4.09±0.342	6.86±0.330	0.59±0.023	0.70±0.122	2.15±0.122	0.32±0.038	---	---	0.76±0.107	9.28±1.033
		(4 3/4–5 1/2)	(3.45–4.62)	(6.22–7.31)	(0.55–0.63)	(0.50–0.92)	(1.93–2.35)	(0.26–0.39)			(0.55–0.89)	(7.93–11.31)
Dorrigo												
QMMO 17146	1	4 1/2	3.70	6.72	0.55	0.67	2.10	0.32	---	---	0.94	7.15
AMC 142438	4	4 1/2+	3.93±0.078	7.02±0.164	0.56±0.003	0.61±0.020	2.04±0.020	0.30±0.008	---	---	0.87±1.055	8.13±0.505
		(4 3/8–4 3/4)	(3.70–4.03)	(6.55–7.31)	(0.55–0.56)	(0.59–0.67)	(2.02–2.10)	(0.29–0.32)			(0.77–1.02)	(7.17–9.17)
AMC 63816	1	4 3/4	4.20	7.39	0.57	0.76	2.18	0.35	---	---	0.89	8.30
Bellinger River												
AMC 142437	1	4 1/2+	3.61	6.72	0.54	0.59	2.02	0.29	---	---	0.81	8.30
Springbrook												
QMMQ 6300	1	4 7/8	3.95	6.89	0.57	0.76	2.18	0.35	---	---	0.85	8.11
Upper Pine Creek												
QMMQ 16903	1	4 3/4+	3.70	7.31	0.58	0.76	2.10	0.32	---	---	0.85	8.60

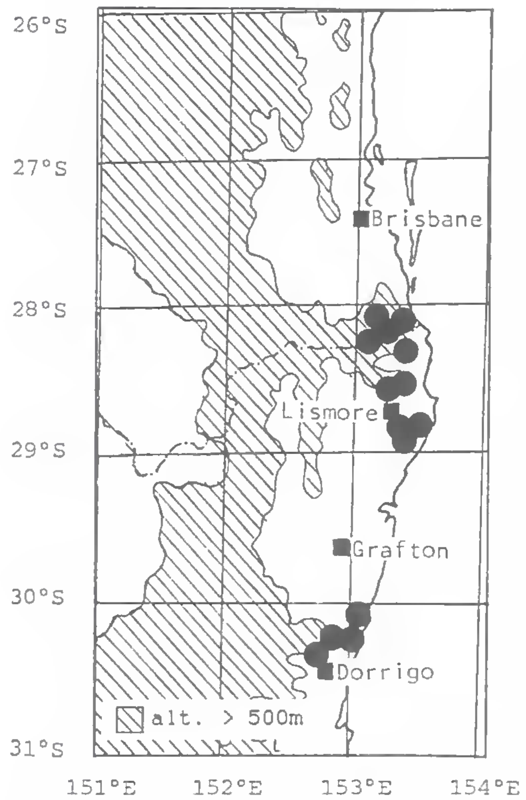


FIG. 17. Distribution of *Ngairea corticicola* (Cox, 1866)

Dorrigo N.P., under bark of fallen tree, rainforest (1, QMMO17142, 6 Mar 1987, J. Stanisic, D. Potter); Booyong Flora Reserve, via Lismore, under bark of fallen trees, rainforest (21, QMMO17005, 9 Mar 1987, J. Stanisic, D. Potter).

SOUTH EAST QUEENSLAND - Lower Ballanjui Falls Circuit, Lamington N.P., litter, NVF (3, QMMO16447, 3 Oct 1985, J. Stanisic, D. Potter); Tullawallal Circuit, Lamington N.P., CNVF (3, QMMO16465, 2 Oct 1985, J. Stanisic, D. Potter); Warrie Circuit, Springbrook N.P., under bark of fallen tree, CNVF (4, QMMO16464, 6 Apr 1986, J. Stanisic); Orchid Bower, Lamington N.P., 900 m, CNVF (8, QMMO6264, Apr 1976, M.J. Bishop); Nagarigoon Falls Circuit, Lamington N.P., CNVF (2, QMMO16463, 20 Apr 1986, J. Stanisic); Warrie N.P., Springbrook, CNVF (28°00'S, 153°00'E) 15, QMMO6300, 4 Oct 1976, M.J. Bishop); Nagarigoon, Lamington N.P., 800 m, CNVF (28°14'S, 153°13'E) (13, QMMO6085, Apr 1976, M.J. Bishop); Mt. Hobwee Circuit, Lamington N.P., litter (3, QMMO16445, 1 Oct 1985, J. Stanisic, D. Potter); Natural Bridge N.P., NVF (28°13'S, 153°14'E) (1, QMMO10456, 18 Mar 1981, ABRS - AM/QM); Tullawallal Circuit, Lamington N.P., litter, NVF (1, QMMO16446, 2 Oct 1986, J. Stanisic, D. Potter); Coomera Falls, Lamington N.P., under bark of fallen tree, CNVF (2, QMMO16461, 19 Apr 1986, J. Stanisic); Slopes of Mt Hobwee, Lamington N.P., under bark of fallen trees, CNVF (17, QMMO16462, 19 Apr 1986, J. Stanisic); Upper Pine Creek, Canungra, under bark, NVF/*Araucaria* (1, QMMO16545, 1 Oct 1986, J. Stanisic, D. Potter; 7, QMMO16903, 21 Jan 1987, J. Stanisic, D. Potter; 3, QMMO16584, 29 Sept 1986, J. Stanisic, J. Chaseling); Araucaria Track, Binna Burra, under bark, NVF (5, QMMO16577, 27 Sept 1986, J. Stanisic); Lower Ballanjui Falls Track, Binna Burra, Lamington N.P., under bark (5, QMMO16550, 25 Sept 1986, J. Stanisic); Coomera Falls Circuit, Binna Burra, Lamington N.P., under bark, NVF (11, QMMO16574, 26 Sept 1986, J. Stanisic).

Diagnosis

Shell depressed, large, diameter 5.88-7.82 mm (mean 6.90 mm), with 4 3/8 to 5 1/2 (mean 4 3/4+) normally coiled whorls. Apex and spire moderately elevated, height of shell 3.36-4.62 mm (mean 3.90 mm). H/D ratio 0.50-0.63 (mean 0.56). Body whorl descending slightly in front, SP/BWW ratio 0.22-0.39 (mean 0.31). Protoconch with 1 5/8 to 2 whorls, mean diameter 1056.8μm at 1 1/2 whorls. Apical sculpture of curved radial ribs crossed by incised spiral lines, most noticeable near the sutures (Fig. 15c). Post nuclear sculpture of low, weak protractively sinuated radial ribs and ridges, occasionally with a vertical periostracal blade (Fig. 15a). interstices 3-5 times their width and without radial riblets. Microsculpture of incised spiral grooves (Fig. 15f). Sculpture reduced on base to almost smooth (Fig. 15b). Base shiny to dull. Umbilicus small, 0.55-1.02 mm (mean 0.81 mm) in diameter, D/U ratio 6.99-11.31 (mean 8.61). Sutures impressed. Whorls flattened above and rounded below the periphery. Body whorl with a weak keel (Fig. 15c), becoming less pronounced in larger specimens. Aperture ovately lunate. Lip simple, slightly thickened at the basal margin, becoming more so at the columella. Columella thickened, twisted and slightly reflected over the umbilicus. Parietal callus pustulose. Colour creamy-white to yellow-horn, upper surface with regular brown-red flammulations fading at the periphery, base creamy-white. Based on 34 measured specimens.

Vas deferens giving rise to a long, muscular epiphallus (Fig. 16a). Epiphallus reflexing apically to enter the penis through a simple pore (Fig. 16b) surrounded by a spongy pilaster, internally with longitudinal pilasters. Penis (Fig. 16b) slender, cylindrical, muscular, slightly swollen apically, internally with an apical fleshy collar and strongly corrugated, longitudinal pilasters. Penial retractor muscle long, inserting on the epiphallus prior to its entry into the penis.

Radula (Fig. 15d,h) with broad triangular mesocone and reduced ectocones on central tooth.

Based on four dissected specimens (QMMO16462, QMMO6330).

RANGE AND HABITAT

N. corticicola inhabits warm subtropical notophyll vine forests of the coastal lowlands and foothills between Dorrigo and Lismore, the Dorrigo Plateau, and the eastern McPherson Ranges. Its northern limit appears to be Mt Tamborine, SEQ. On the basis of material collected late last century and early this century, it would appear that the Big Scrub formed an important part of the range of *N. corticicola*. In spite of the fact that much of the Big Scrub was cleared by early cedar-getters and more recently for agriculture, *N. corticicola* is still common in some of the remnants e.g. Booyong Flora Reserve, near Lismore, NSW. The species lives under the bark of rotting logs.

REMARKS

Southern representatives of *N. corticicola* (QMMO17146, AMC142438) have comparatively lower whorl counts than northern specimens (Table 4).

Mussonula Iredale, 1937

Mussonula Iredale, 1937b,p. 13

TYPE SPECIES

Mussonula verax Iredale 1937; by original designation.

PREVIOUS STUDIES

Iredale (1937b) related *Mussonula* to *Paralaoma* Iredale, 1913 which is a punctid group with a spirally lirate protoconch. Although Iredale (1937b) noted spirals in *M. verax* he failed to notice the less conspicuous apical radial elements referred to in this study (Figs 18d, 20f). Combined with general shell sculpture and details of the radula (Fig. 20d, e), the apical sculpture places *Mussonula* in the Charopidae.

DIAGNOSIS

Shell small to moderately large, trochoid, adult shell diameter range 4.81-5.63 mm, with 3 7/8 to 4 1/8 normally coiled whorls, last whorl descending. Height of shell 3.32-4.45 mm. Apex and spire strongly elevated. Protoconch strongly exsert. Apical sculpture of numerous bold (*verax*) to fine (*fallax*) spiral cords, and very weak radial ridges which become more prominent near the nuclear-post nuclear junction. Post apical sculpture of numerous, high, protractively sinuated radial ribs with periostracal blades inclined toward the shell apex. Some trace of weak incised spiral lines (*fallax*) but no microriblets present. Sculpture continuous on the base. Umbilicus narrow U-shaped. Sutures impressed. Whorls rounded above and below a strongly angulate periphery. Aperture subquadrate. Lip simple, columella reflected slightly toward umbilicus. Colour yellow-horn to brown with adhering dirt particles.

Pallial cavity with incomplete secondary ureter and kidney with vestigial rectal lobe. Genitalia unknown. Radula as for *Mussonula fallax*.

DISTRIBUTION AND ECOLOGY

Mussonula extends from Byangum on the Richmond River, northern NSW to the Gympie forestry area, SEQ. It inhabits moist lowland notophyll vine forest in the south, and drier microphyll vine forest (with *Araucaria*) and vine thicket in the north. The two species are allopatric.

Little is known of the microhabit for although C.T. Musson collected the type series of *M. verax* arboreally, and a single live specimen of *M. fallax* was found under timber among rocks, all other specimens have come from litter samples. The trochoid shell and dark animal colour indicate an arboreal or semi-arboreal existence. However the adhering dirt particles on the shell suggest that it is a ground dweller. Possibly it lives among friable earth, between and under rocks, and forages for food on vertical surfaces above the ground.

COMPARISONS

The extremely prominent radial ribs (Figs 18c, 20g), strongly angulate periphery, elevated spire, exsert protoconch with strong spiral cords (Figs 18d, 20f), and almost total lack of micros-

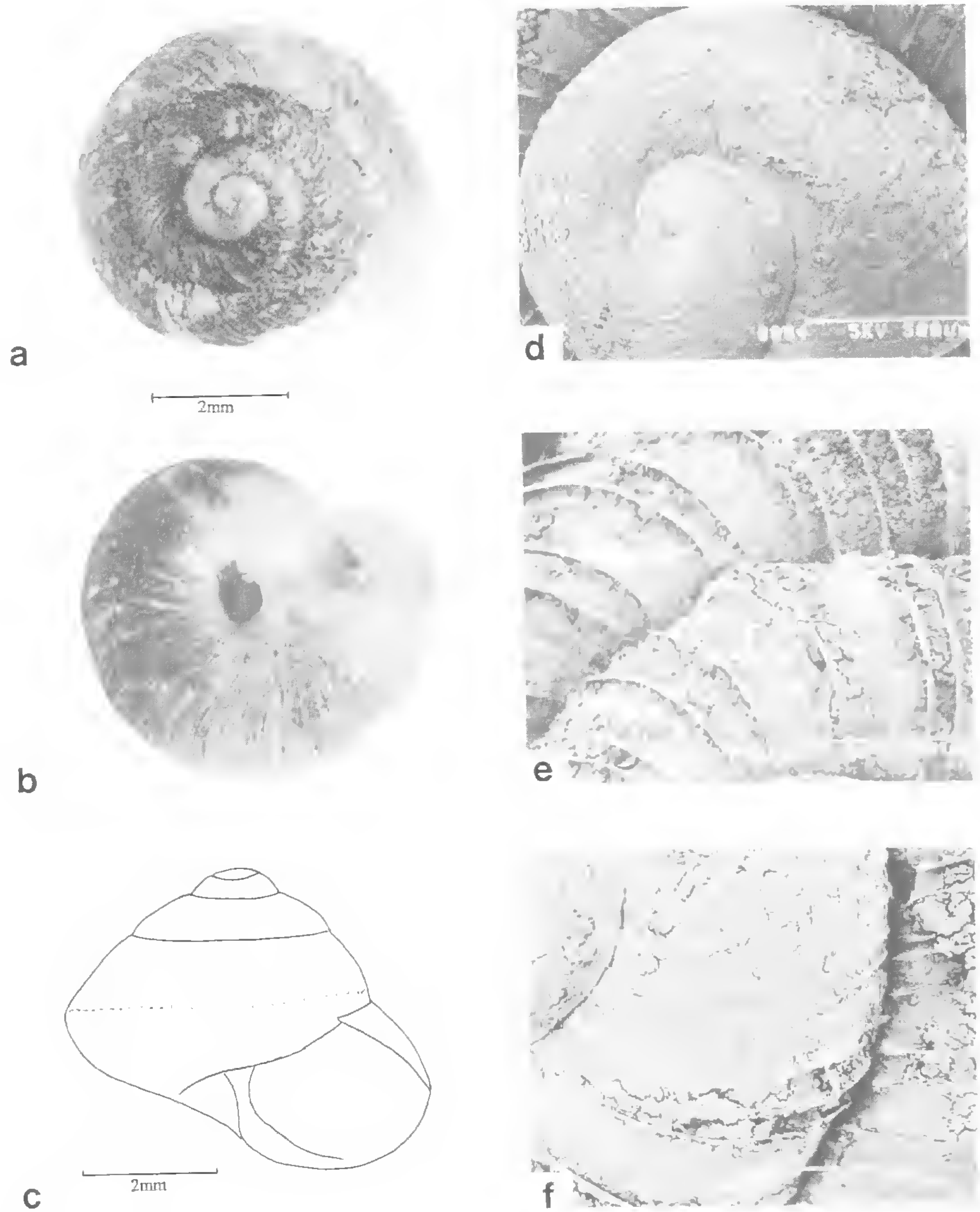


FIG. 18. *Mussonula verax* Iredale, 1937. a–c, Scrub at North Pine, SEQ. AMC63770. holotype; d–f, c. 2km E of summit, Mt Nebo, SEQ. QMMO16518. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, terminal region of protoconch. Scale lines as marked.

culpture in *Mussonula* are a combination of features not found in any other east coast charopid. *Oreokera* Stanisic, 1987, from north Queensland has the same shape and postnuclear ribbing as *Mussonula* but is larger and has quite prominent, reticulate microsculpture (Stanisic, 1987, pls 1c,d;2c,d,e). *Hedleyoconcha* Pilsbry, 1893 has a similar shaped shell but has strong reticulate sculpture and a punctate protoconch (Figs 23e, f; 26d).

Mussonula verax Iredale, 1937
(Figs 18–19; Tables 2, 5)

Thalassia delta (Pfeiffer); Hedley and Musson, 1892, p. 553 - misidentification.
Mussonula verax Iredale, 1937b, p. 13, pl. 1, fig. 11.

COMPARISONS
M. verax can be distinguished from *M. fallax* by its larger size and bolder, more regular, apical spiral cords (Figs 18d, 20f). *Ngairea levicostata* has a similar shell to *M. verax* but is slightly larger with apical sculpture of curved radial ribs and weak spiral cords (Fig. 6d); *N. dorrigoensis* which is sympatric with *M. verax* in the southern part of the D'Aguilar Range, SEQ, is larger, has a less elevated spire, and microsculpture of prominent spiral cords (Fig. 3e).

TYPE MATERIAL
HOLOTYPE: AMC63501, in scrubs, arboreal, North Pine River, South Queensland. Coll. C.T. Musson. Height of shell 4.54 mm, diameter 5.46 mm, H/D ratio 0.82, D/U ratio 13.29, whorls 3 7/8+.
PARATYPES: AMC63770, 5 specimens. Scrub at North Pine, SEQ. Coll. by C.T. Musson.

OTHER MATERIAL
Fred's Rd, Mt Mee, SEQ, rainforest, leaf litter, (27°05'S, 152°43'E) (1, QMMO7340, 14 Apr 1980, J. Stanisic, N. Hall, A. Green); Mt Nebo, SEQ, c. 2 km E of summit, NVF/*Araucaria*, leaf litter (27°24'S, 152°47'E) (1, QMMO16518, 13 Aug 1980, J. Stanisic); Wratten's Camp, Wrattens S.F., SEQ, NVF, litter (26°17'S, 152°20'E) (1, QMMO11500, 17 Jul 1980, J. Stanisic, A. Green); c. 0.5 km E of Mt Mia turnoff on Mt Mia - Kilkivan Rd, SEQ (26°15'S, 152°27'E) (1, QMMO12320, 1 Sept 1982, AM/QM - ABRS 1982); Maiala N.P., Mt Glorious, SEQ, NVF (1, QMMO11602, 20 Jun 1982, MSA Party).

DIAGNOSIS
Shell trochoid, small, diameter 5.04–5.63 mm (mean 5.36 mm) with 3 7/8 to 4 (mean 4-) loosely coiled whorls. Apex and spire strongly elevated, height of shell 4.03–4.45 mm (mean 4.31 mm), H/D ratio 0.79–0.82 (mean 0.81). Body whorl descending more rapidly. SP/BWW ratio 0.52-0.57 (mean 0.54). Protoconch strongly exsert with 1 1/2 to 1 1/2+ whorls, mean diameter 1370.5 μm at 1 1/2 whorls. Apical sculpture of about 20 continuous spiral cords and curved radial ridges appearing in the last 1/8 whorl (Fig. 18d). Post nuclear sculpture of high, crowded protractively sinuated radial ribs, 90–120 (mean 104.8) on the body whorl (Fig. 18c). Ribs/mm 5.68-6.78 (mean 6.20). Major ribs with slender backward curved periostracal blades, interstices 7-20 times their width, no radial riblets. Microsculpture absent. Sculpture continuous on the base (Fig. 18b). Umbilicus very narrow, U-shaped, slightly obscured, diameter 0.31–0.41 mm (mean 0.35 mm), D/U ratio 13.29–17.19 (mean 15.27). Sutures impressed. Whorls rounded above and below an angulate periphery. Aperture subquadrate. Lip simple, columella twisted, vertical, slightly covering the umbilicus. Parietal callus pustulose, well developed. Colour yellow-horn with adhering dirt particles. Based on 4 measured adults. Anatomy unknown.

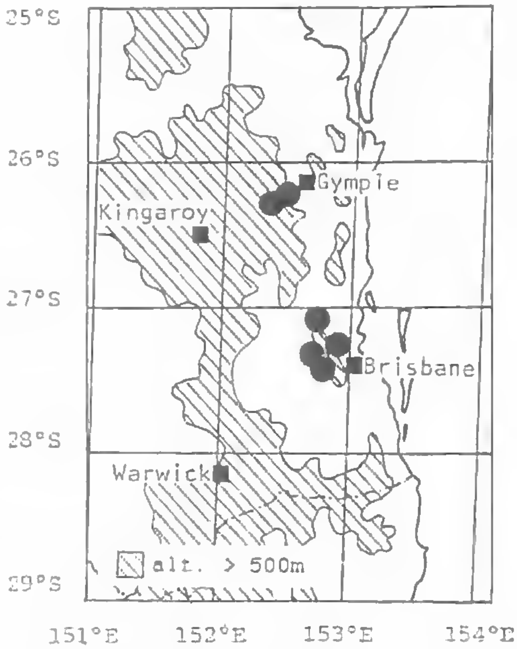


FIG. 19. Distribution of *Mussonula verax* Iredale, 1937.

TABLE 5 - LOCAL VARIATION IN *MUSSONULA VERAX* IREDALE, 1937 AND *MUSSONULA FALLAX* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Mussonula verax North Pine Scrubs AMC 63501 (Holotype)	1	3 7/8+	4.45	5.46	0.82	1.01	1.93	0.52	112	6.52	0.41	13.29
AMC 63770	2	4 (4–4+)	4.16±0.130 (4.03–4.29)	5.17±0.707 (5.04–5.29)	0.81±0.005 (0.80–0.81)	0.97±0.045 (0.92–1.01)	1.81±0.040 (1.77–1.85)	0.54±0.015 (0.52–0.55)	93.5±3.50 (90–97)	6.33±0.645 (5.68–6.97)	0.32±0.010 (0.31–0.33)	16.26±0.930 (15.33–17.19)
Mt Mia QMMO 12320	1	4+	4.45	5.63	0.79	1.01	1.77	0.57	120	6.78	closed	--
Mussonula fallax Byangum AMC 63870 (Holotype)	1	4 1/8	3.41	5.32	0.64	0.72	1.62	0.45	--		0.86	6.18
Huonbrook AMC 142449	1	4 1/8-	3.32	4.81	0.69	0.64	1.62	0.39	-		0.82	5.86

RANGE AND HABITAT

M. verax inhabits notophyll vine forests of the D'Aguilar Range and drier microphyll vine forests of the Gympie region, SEQ.

REMARKS

C.T. Musson collected this species during an expedition to SEQ in 1887 which was funded by noted malacologist Dr J.C. Cox. The species was misidentified as *Thalassia delta* (Pfeiffer, 1857) by Hedley and Musson (1892). Iredale (1937b, p. 13) noted the error and erected the genus. Although the type locality of the species is given broadly as "scrubs at North Pine River", the itinerary of Musson's trip suggests that a more specific locality may be Mt Mee, SEQ.

Mussonula fallax sp. nov.
(Figs 20–22; Tables 2, 5)

ETYMOLOGY

Latin *fallax*, fallacious; referring to its having been previously identified as *M. verax*.

COMPARISONS

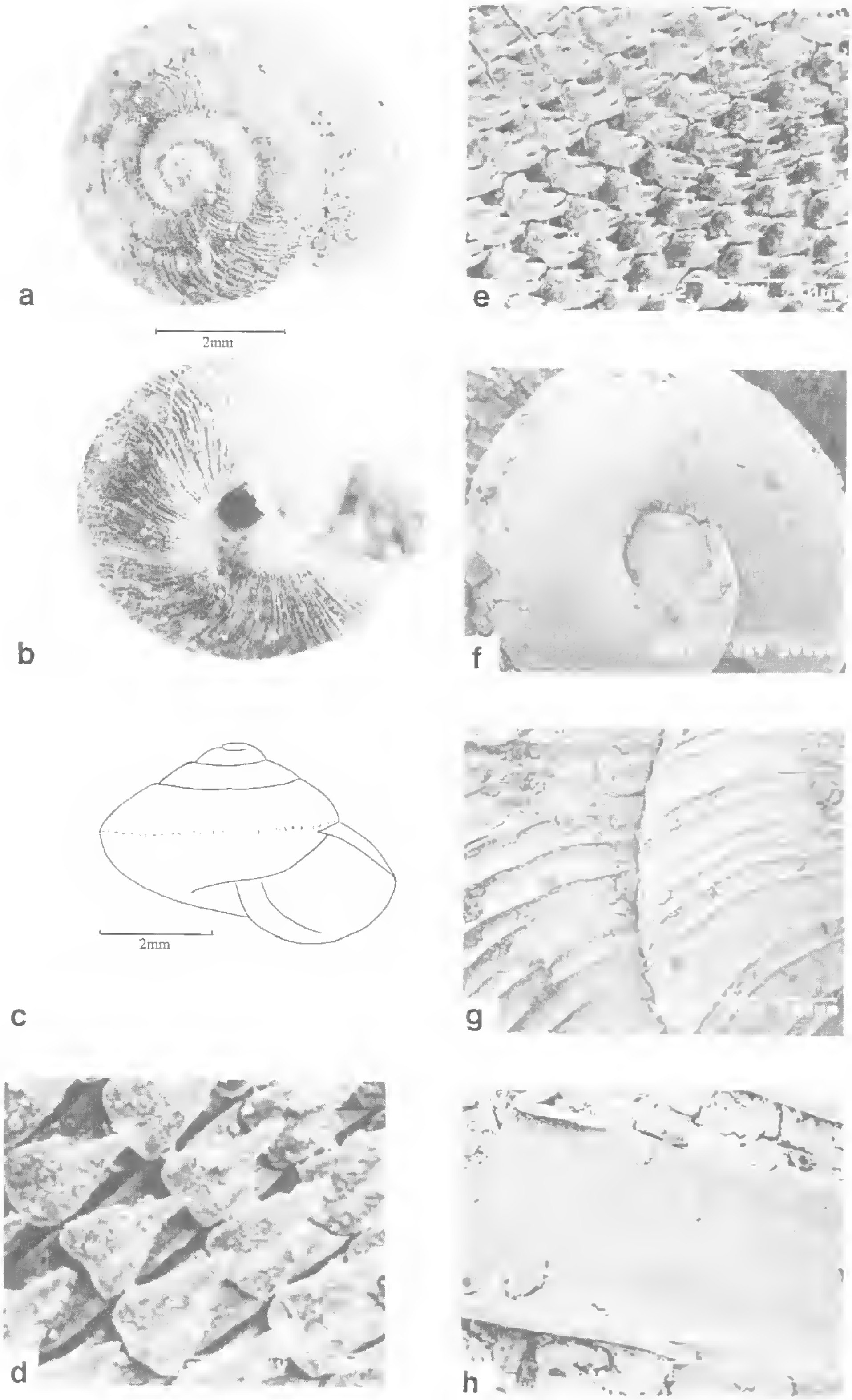
M. fallax differs from *M. verax* by having finer, more irregular apical spiral cords (Fig. 20f) and a smaller shell. *Hedleyoconcha delta* (Pfeiffer, 1857) has a trochoid shell but is much larger with greatly elevated spire and has postnuclear sculpture of low radial ribs and spiral cords in a reticulate pattern (Fig. 23e, f).

TYPE MATERIAL

HOLOTYPE: AMC63870, No. 1 Scrub at Byangum, NSW, Cox coll. Height of shell 3.41 mm, diameter 4.32, H/D ratio 0.64, D/U ratio 6.18, whorls 4 1/8-.
PARATYPES: Mt Warning N.P., NSW (28°24'S, 153°16'E) (1, AMC129289, 18 Mar 1981, ABRS - AM/QM); Upper Coopers Ck, Huonbrook, NSW (1, AMC142449, 26 Aug 1936, A. Musgrave, E. Troughton); Burleigh Heads N.P., SEQ, vine thicket (4, QMMO6157, QMMO6160, Oct 1976, M.J. Bishop); Terania Ck, NENSW, NVF, under piece of wood among rocks (1, QMMO17323, Aug 1987, J. Stanisic); Richmond Rv., NSW (1, AMC142448).

DIAGNOSIS

Shell small, trochoid, diameter 4.81–5.32 mm (mean 5.07 mm) with about 4 1/8- normally coiled whorls, last whorl only slightly descending. Apex and spire strongly elevated, SP/BWW ratio 0.39–0.45 (mean 0.42), height 3.32–3.41 mm (mean 3.37). H/D ratio 0.64–0.69 (mean 0.67). Protoconch exsert, slightly shiny with 1


a
2mm
e
b
f
2mm
c
g
d
h

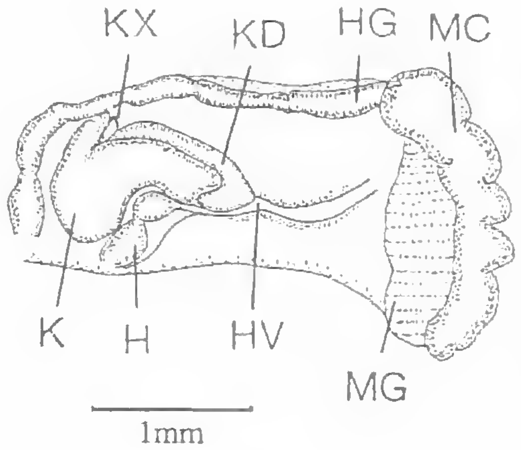


FIG. 21. *Mussonula fallax* sp. nov. Terania Creek, NSW, QMMO17323, paratype, Pallial cavity. Scale line as marked.

1/2-1 5/8- whorls, mean diameter 1149.5μm at 1 1/2 whorls. Apical sculpture of 20–25 interrupted spiral cords with numerous, low, curved radial ridges forming toward the end of the protoconch (Fig. 20f). Post nuclear sculpture of numerous, high, protractively sinuated radial ribs, with periostracal blades which are folded toward the apex (Fig. 20g). No microriblets. Microsculpture consisting of vague incised spiral lines (Fig. 20g). Sculpture continued on the base (Fig. 20b). Rib interstices variable, 5-15 times the width of the ribs. Umbilicus narrow, V-shaped, diameter 4.81–5.32 mm (mean 5.07 mm), D/U ratio 5.86–6.18 (mean 6.02). Sutures impressed. Whorls rounded above and below a strongly angulate periphery. Lip simple, columella dilated and slightly twisted toward the umbilicus. Aperture subquadrate. Parietal callus strongly developed. Colour brown, often covered with dirt particles. Based on 2 measured adults.

Foot and tail short and broad, bluntly tapering posteriorly. Body colour dark with sides of foot and outer margins of the sole purple-grey. Upper body and neck black. Ommatophores purple-grey. Pallial roof black. Pallial cavity occupying c. 1/2 whorl apically. Mantle collar well developed with large glandular zone extending onto the lung roof. Kidney with triangular pericardial lobe and rectal lobe present as a tiny vestige abutting hindgut. Ureter sigmurethrous without complete secondary branch. Ureteric pore situated adjacent to the hindgut, anterior to the small rectal lobe of the kidney (Fig. 21). Reproductive organs immature.

Central tooth of radula (Fig. 20d,e) with lanceolate mesocone and small, pointed ectocones; inner laterals with endocone absent and more prominent ectocone. Outer laterals and marginals typical.

Based on one dissected subadult (QMMO17323).

FIG. 20. *Mussonula fallax* sp. nov. a–c, No. 1 scrub at Byangum, NSW, AMC63870, holotype; d–e, Terania Ck, NSW, QMMO17323, paratype; f–h, Burleigh Heads N.P., SEQ, QMMO 6157, paratype. a–c, entire shell; d, central and lateral teeth; e, marginal teeth; f, apical sculpture; g, post nuclear sculpture; h, details of post nuclear microsculpture. Scale lines as marked.

RANGE AND HABITAT

M. fallax inhabits the notophyll vine forests of the moist foothills of coastal northern NSW, and the unusual coastal vine thicket at Burleigh Heads, SEQ. Its microhabitat is not fully known.

REMARKS

In the absence of data on the terminal genitalia the two species are separated on the difference in protoconch sculpture. Habitat destruction, particularly in the Big Scrub area of north-eastern NSW, has had significant effects on the distribution of *M. fallax*. Iredale (1941b, p. 2) cited specimens of *M. verax* from the Richmond River, northern NSW. These are *M. fallax*.

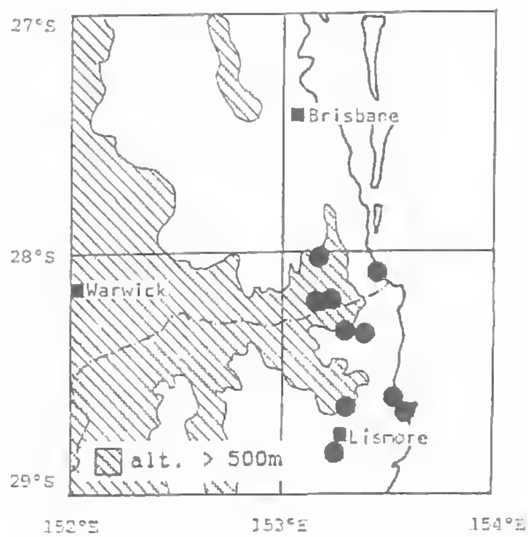


FIG.22. Distribution of *Mussonula fallax* sp. nov.

Hedleyoconcha Pilsbry, 1893

Hedleyoconcha Pilsbry, 1893, p.18; Iredale, 1937a, p. 321; Iredale, 1937b, p. 13; Iredale, 1941a, p. 264; Iredale, 1942, p. 35; Iredale, 1944, p. 317; Burch 1976, p.133.

TYPE SPECIES

Helix delta Pfeiffer, 1857: by original designation.

PREVIOUS STUDIES

Pilsbry (1893) placed *Hedleyoconcha* in the Flammulinidae where it remained until Iredale (1942) erected the Hedleyoconchidae for it. Solem (1983) included Hedleyoconchidae with his expanded Charopidae. I follow Solem and consider that *Hedleyoconcha* can be derived from more generalised charopids.

DIAGNOSIS

Shell relatively large, diameter 5.38-10.08 mm with 5 1/8 to 6 5/8 whorls. Spire and apex strongly elevated (Figs 23c, 26c), height of shell 4.62-6.47 mm, last whorl descending. Protoconch of 1 1/2 to 1 3/4 whorls, pitted (Fig. 23c). Post nuclear sculpture of low, protractively sinuated, radial ribs and low rounded spiral cords in a reticulate pattern (Figs 23f, 26d). Sculpture altered after 4 whorls, continuous on base but much less pronounced (Figs 23b, 26b). Umbilicus narrow, partially obscured by the reflected columella. Sutures lightly impressed. Whorls slightly flattened above and rounded below a strongly angulate to thread-carinate periphery. Aperture ovately lunate. Lip simple, columella dilated and slightly reflected over the umbilicus. Colour straw to cream-yellow with a darker spire. Periostracum deciduous.

Foot and tail broad, rounded posteriorly. Caudal horn present. Colour creamy-white with some pigmentation on the pallial roof. Ommatophores black. Kidney elongate, vaguely triangular with a reduced rectal lobe. Ureter sigmurethrous with an incomplete secondary branch. Ureteric opening in the angle between the kidney lobes. Ovotestis several clumps of palmately clavate lobes of alveoli, oriented at right angles to the plane of coiling. Terminal male genitalia with thin vas deferens and large, reflexed, muscular epiphallus, entering penis through a large fleshy pilaster opposite a grooved muscular thickening which acts as a collar. Penis proper with long slender corrugated pilasters. Penial retractor muscle inserted at the penis-epiphallus junction. Radula with tricuspid central and lateral teeth which have long mesocones, short endo- and ectocones, and well-developed anterior flares; marginals typical.

DISTRIBUTION AND ECOLOGY

Hedleyoconcha has a classic relict distribution with a widespread species in northern NSW and southern Queensland, an altitudinally restricted species on the summit of Mt Bellenden-Ker in north Queensland and a further species on Lord Howe Island, off the coast of New South Wales. Although similar distribution patterns are seen among some flightless groups of insects such as the Peloridiidae (Monteith, 1980) this is the first time a land snail group has been identified as having such an unusual and biogeographically complex distribution.

COMPARISONS

The high spire, punctate apical sculpture (Fig. 23e) and distinctive low reticulate post nuclear sculpture (Figs 23f, 26d) distinguish *Hedleyoconcha* from other subtropical and tropical charopids. *Oreokera* Stanisic, 1987 has an elevated spire but apical sculpture of spiral cords, prominent post nuclear radial ribs and fine, reticulate microsculpture (Stanisic, 1987, pls 1,2). *Mussonula* is much smaller and has prominent apical spiral cords (Figs 18d, 20f) and crowded, high, curved radial ribs on the post nuclear whorls (Figs 18e, 20g). *Ngairea* lacks the punctate apical sculpture seen in *Hedleyoconcha* and has much finer post apical sculpture (Figs 3e, 6e, 9g, 12e, 15f).

The species show minor differences in shell features but are readily segregated on the basis of geography.

KEY TO SPECIES OF *HEDLEYOCONCHA*

1.Shell with umbilicus wider (Fig. 26g), mean D/U ratio 4.60; Lord Howe Id .... *addita*

Shell with umbilicus narrower, mean D/U ratio greater than 6.50 2

2.Shell with strong reticulate sculpture on early whorls (Fig. 26d); protoconch weakly punctate (Fig. 26d); Mt Bellenden Ker, NEQ ....*ailaketoae*

Shell with weaker reticulate sculpture on early whorls (Fig. 23f); protoconch strongly punctate (Fig. 23e); southern Queensland and northern New South Wales .... *delta*

Hedleyoconcha delta (Pfeiffer, 1857)
(Figs 23–25; Tables 2, 6)

Helix delta Pfeiffer, 1857, p. 386

Helix conoidea Cox, 1864, p. 21; non Draparnaud, 1801.

Helix fenestrata Cox, 1866, p.374; non Sowerby, 1841.

Charopa (Thalassia) delta (Pfeiffer); Tryon, 1886, p. 215, pl. 63, fig. 76.

Flammulina (Hedleyoconcha) delta (Pfeiffer); Pilsbry, 1893, pp.18-19.

Hedleyoconcha delta (Pfeiffer); Iredale, 1937a, p. 321; Iredale, 1941a, p. 35.

Hedleyoconcha duona Iredale, 1937b, p. 13, pl.1, fig. 13; Iredale, 1941a, p. 35, fig. 9.

COMPARISONS

H. delta can be distinguished from *H. ailaketoae* by its larger size, less prominent adult sculpture and more conspicuous apical sculpture. Anatomically the differences are minor with slightly more corrugated penial pilasters and a more prominent apical penial bulb present in *H. ailaketoae* (Fig. 27a–b). *H. delta* is not easily confused with any sympatric charopids. *Mussonula verax* (Fig. 18), *M. fallax* and *Ngairea levicostata* all have elevated shells and occur in the NSW-QLD border areas. However they have prominent, fine, crowded radial ribs on the adult shell whorls (Figs 6e, 18e, 20g), spiral cords (with radials in *N. levicostata*) on the protoconch (Figs 6d, 18d, 20f), are smaller, and have a less prominent peripheral keel (Figs 6c, 19c, 20c). *Ngairea murphyi* resembles *H. delta* in gross conchological detail but is smaller, with more tightly coiled whorls, less elevated spire, more open umbilicus, finer adult sculpture and apical sculpture of fine pits and wrinkles (Fig. 9a, b, e–g).

H. delta is microsympatric with several helicinids - *Pleuropoma jana* (Iredale, 1937) from the Port Macquarie area, NSW and *P. draytonensis* (Pfeiffer, 1857) from far northern NSW and southern Queensland. Both species have elevated shells similar in colour to *H. delta* and live on the leaves of low shrubs. However they may be distinguished in having strongly incised spiral grooves on the protoconch and adult whorls, and no umbilicus. The introduced and widespread Pacific helicarionid *Coneuplecta calculosa* (Gould, 1852) is also microsympatric with *H. delta* in parts of northern NSW and southern Queensland but it is much smaller, transparent, yellow-horn in colour, and has a microsculpture of numerous fine incised spiral lines.

PREVIOUS STUDIES

H. delta was originally described from the Drayton Range (= Toowoomba), SEQ. Cox (1864, 1866) introduced names for two NSW populations (*conoidea* and *fenestrata*) which he later (Cox, 1868) synonymised with *H. delta*. Iredale (1937a) placed them in synonymy with *Helix scandens* Cox, 1872, a helicarionid, then (1937b) realised the error but considered the NSW specimens specifically separate as *H. duona* on the basis of their broader base, narrower umbilicus and weaker sculpture.

In this study specimens of *Hedleyoconcha* were dissected from numerous localities (including Wentworth Falls, west of Sydney, NSW) and no perceptible differences in genital anatomy were noted. Differences in shell size and sculpture are mosaic and fall within the range of a single widely distributed species. Hence Iredale's separation is considered unsustainable and *H. duona* is placed in synonymy with *H. delta*.

TYPE MATERIAL

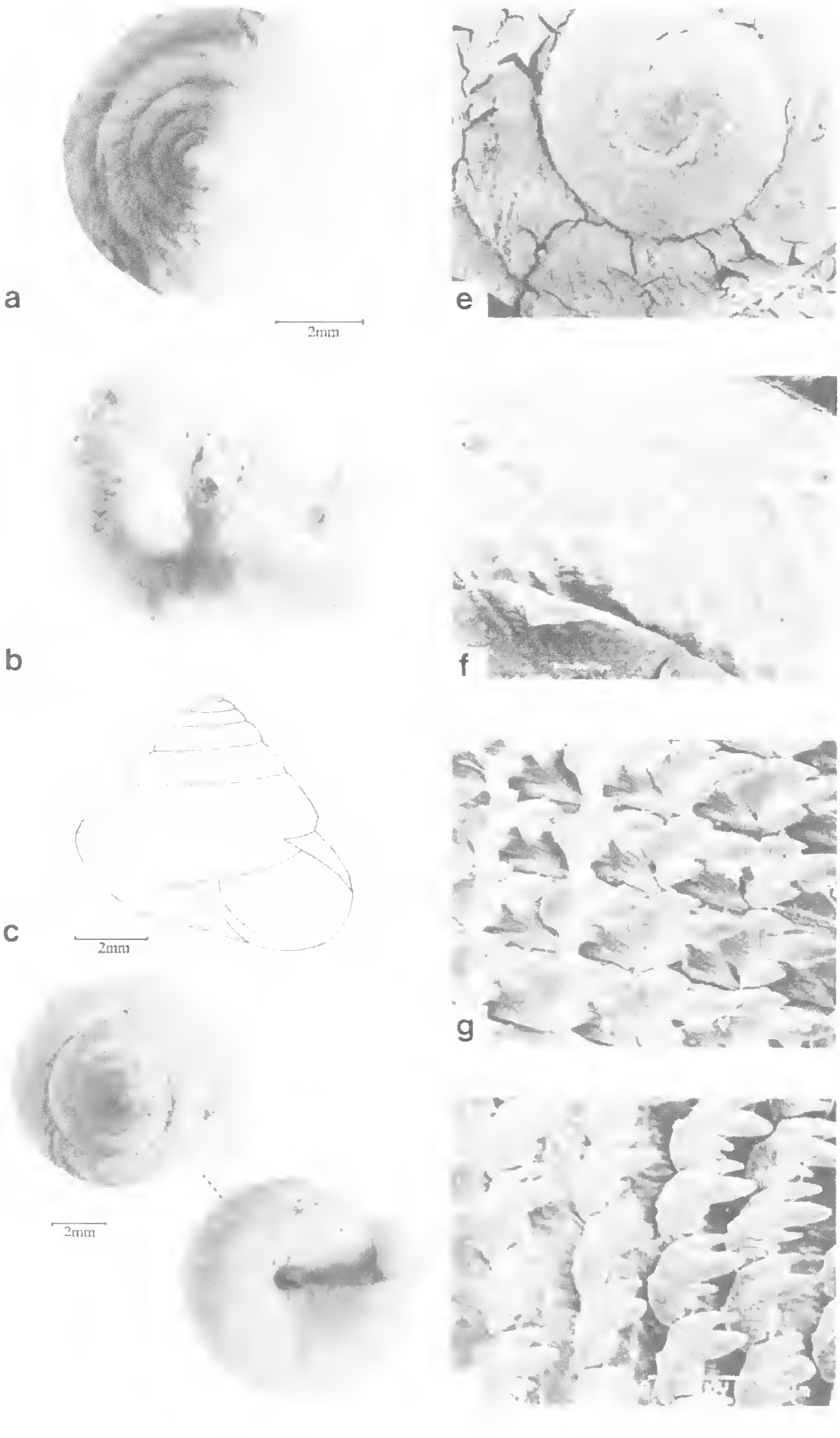
LECTOTYPE: BMNH1982246, Drayton Range, North Australia. Collected by Mr Stutchbury, ex H. Cuming collection. Height of shell 6.64 mm, diameter 7.56 mm, H/D ratio 0.88, D/U ratio 7.67, whorls 6 1/4.

PARALECTOTYPES: BMNH1982246, 2 specimens, same collection data as lectotype.

HOLOTYPE of *duona*: AMC63526, Terrigal, near Gosford, NSW. No other data. Height of shell 6.30 mm, diameter 8.40 mm, H/D ratio 0.75, D/U ratio 10.24, whorls 6.

OTHER MATERIAL

NEW SOUTH WALES: Frank's land, Terrigal, Gosford, in scrub, on trees (2, AMC142450, S.W. Jackson, 23 Mar 1913); Dungog S.F., among orchid roots on fallen tree (1, AMC142455, W. Dowling, 19 Jun 1962); Lismore (1, AMC142458, Lower); In valley down Wentworth Falls, rainforest by creek (1, AMC142453, D.K. McAlpine); Sassafras Gully, Springwood (2, AMC142452, C.F. McLauchlan, 8 May 1948); Dorrigo Scrubs, on underside of leaves on trees (2, AMC142454, Dec 1910, S.W. Jackson); Byron Bay scrubs (7, AMC142457, 1904, S.W. Jackson); 11.4 km S of Nymboida, on Grafton-Armidale


a
2mm
e
b
f
c
2mm
g
2mm

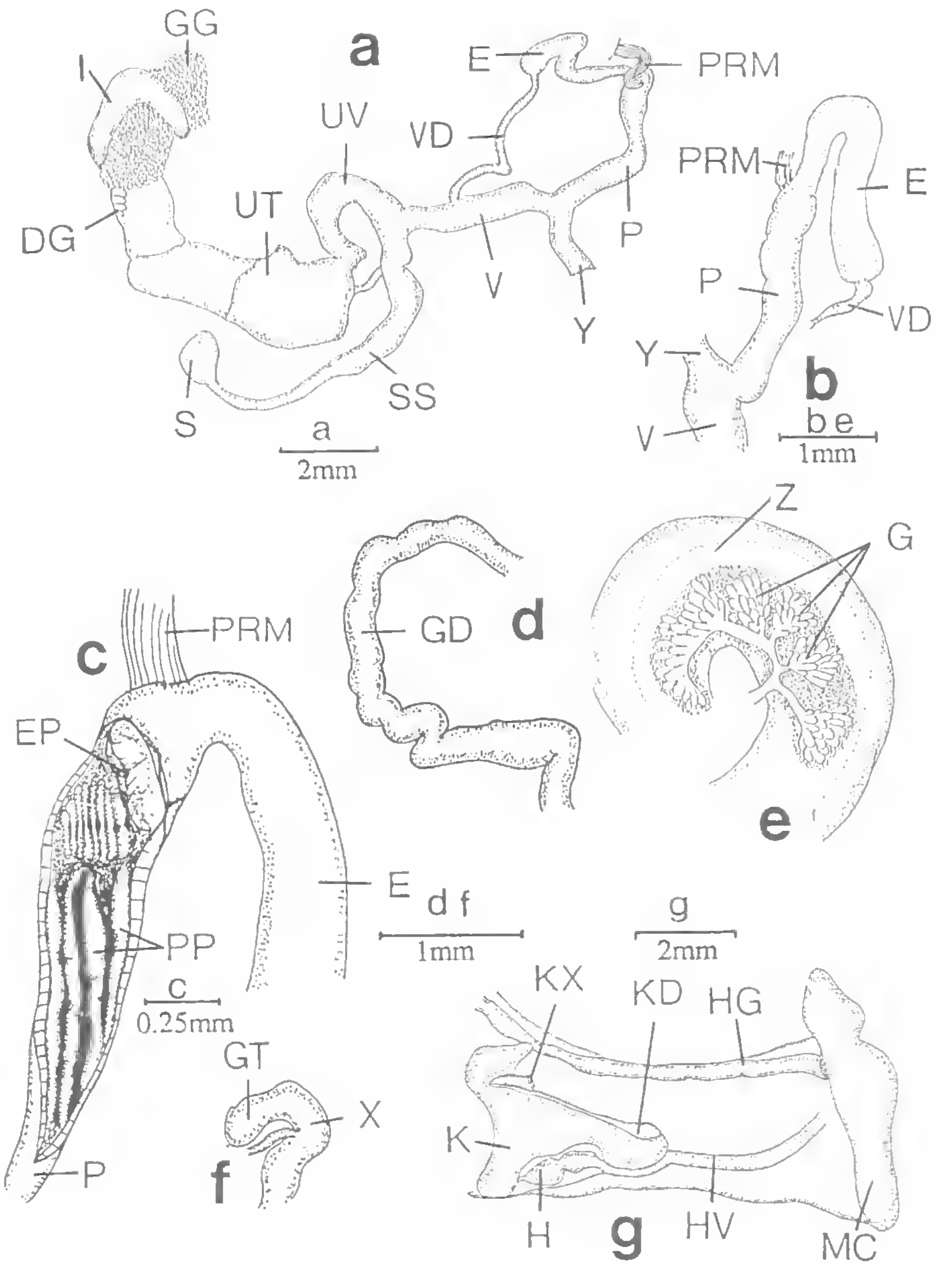


FIG. 24. *Hedleyoconcha delta* (Pfeiffer, 1857). Dandabah, Bunya Mts, SEQ, QMMO6068. a, genitalia; b, details of penis/epiphallus region; c, details of penis interior; d, hermaphroditic duct; e, ovotestis; f, talon; g, pallial cavity.

FIG 23. *Hedleyoconcha delta* (Pfeiffer, 1857). a–c, Drayton Range, North Australia. BMNH1982246, lectotype; d. Terrigal, near Gosford, NSW. AMC63526, holotype of *duona*: e–h, Dandabah, Bunya Mts, SEQ. QMMO6068. a–d, entire shells; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale line as marked.

TABLE 6 - LOCAL VARIATION IN *HEDLEYOCONCHA DELTA* (PFEIFFER, 1857), *HEDLEYOCONCHA AILAKETOAE* SP. NOV. AND *HEDLEYOCONCHA ADDITA* IREDALE, 1944 (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Hedleyoconcha delta												
Drayton Range BMNH 19822246 (Lectotype)	1	6 1/4	6.64	7.56	0.88	2.19	2.77	0.36	---	---	0.99	7.67
Bunya Mts QMMO 6068	3	6 1/8+ (5 7/8-to 6 5/8)	6.53±0.733 (5.63–7.98)	8.82±0.642 (7.98–10.08)	0.74±0.027 (0.71–0.79)	1.85±0.256 (1.51–2.35)	2.55±0.103 (2.35–2.69)	0.72±0.078 (0.64–0.88)	---	---	1.13±0.207 (0.92–1.54)	8.09±0.783 (6.55–9.09)
QMMO 12295	4	6 1/4 (6 – 6 3/8+)	6.47±0.149 (6.22–6.89)	8.30±0.373 (7.82–9.41)	0.78±0.021 (0.73–0.83)	1.91±0.071 (1.77–2.10)	2.65±0.023 (2.61–2.69)	0.72±0.021 (0.68–0.78)	---	---	1.00±0.028 (0.92–1.03)	8.34±0.619 (7.61–10.19)
Beaury S.F. OMMO 10941	1	6 3/8	5.97	7.65	0.78	1.93	2.52	0.77	---	---	0.68	11.28
Richmond Range QMMO 6266	3	5 7/8+	5.21±0.046 (5.13–5.29)	6.36±0.074 (6.22–6.47)	0.82±0.006 (0.81–0.83)	1.51±0.049 (1.43–1.60)	2.38±0.030 (2.35–2.52)	0.64±0.026 (0.59–0.68)	---	---	0.62	10.32±0.123 (10.09–10.50)
Bruxner Park F.R. QMMO 16783	2	6+ (6 –6 1/8+)	5.30±0.255 (5.04–5.55)	7.27±0.290 (6.98–7.56)	0.73±0.005 (0.72–0.73)	1.48±0.125 (1.35–1.60)	2.61±0.085 (2.52–2.69)	0.57±0.065 (0.50–0.63)	---	---	0.75±0.030 (0.72–0.78)	9.70
Port Macquarie OMMO 16793	1	6	5.63	7.14	0.79	1.77	2.61	0.68	---	---	0.88	8.90
Terrigal AMC 63526	1	6	6.30	8.40	0.75	1.85	2.69	0.69	---	---	0.82	10.24
AMC 142450	2	6+ (5 7/8-to6 1/4)	5.59±0.545 (5.04–6.13)	7.48±0.590 (6.89–8.07)	0.75±0.015 (0.73–0.76)	1.60±0.335 (1.26–1.93)	2.48±0.130 (2.35–2.61)	0.64±0.100 (0.54–0.74)	---	---	0.82±0.100 (0.72–0.92)	9.16±0.425 (8.73–9.58)
Wentworth Falls AMC 26350	2	6 3/8 (6 1/4–6 1/2-)	6.43±0.040 (6.39–6.47)	8.24	0.79±0.005 (0.78-0.79)	1.77	2.90±0.040 (2.86–2.94)	0.61±0.010 (0.60–0.62)	---	---	1.00±0.030 (0.97–1.03)	8.28±0.255 (8.02–8.53)
Hedleyoconcha ailaketoae												
Mt Bellenden Ker QMMO 11254 (Holotype)	1	5 1/8+	5.13	6.81	0.75	1.43	2.27	0.63	---	---	0.72	9.47
QMMO 15802	1	5 1/8	4.62	5.97	0.77	1.35	2.27	0.59	---	---	0.72	8.30
Hedleyoconcha addita												
Lord Howe Is. AMC 63488 (Lectotype)	1	6	5.46	6.89	0.79	1.43	2.27	0.63	---	---	1.48	4.66
AMC 150093	1	6 1/8	6.38	6.98	0.77	1.51	2.27	0.67	---	---	1.54	4.53

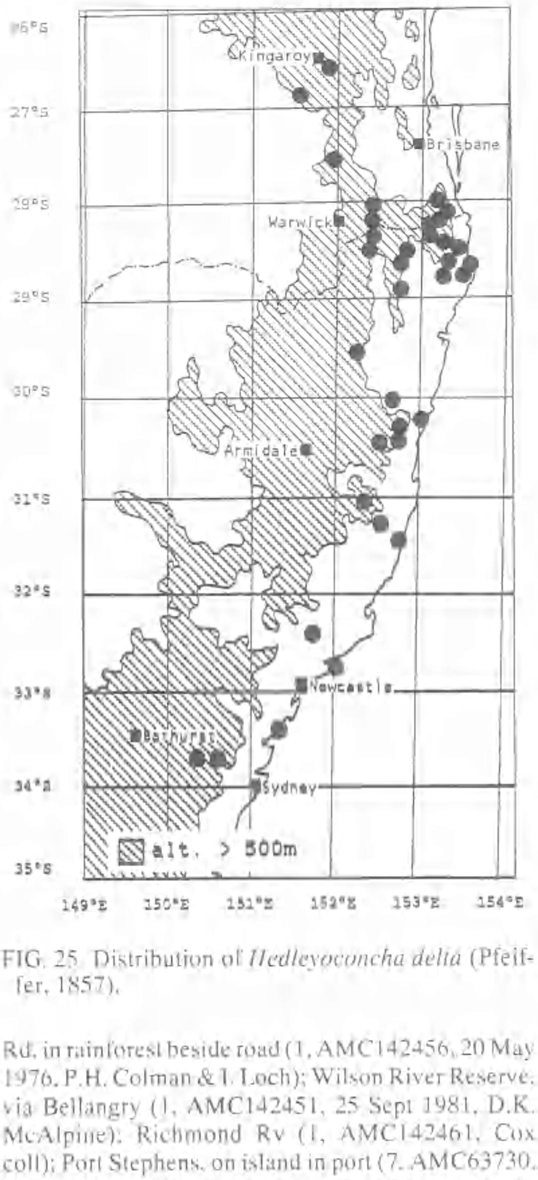


FIG. 25. Distribution of *Hedleyoconcha delta* (Pfeiffer, 1857).

Rd, in rainforest beside road (1, AMC142456, 20 May 1976, P.H. Colman & I. Loch); Wilson River Reserve, via Bellangry (1, AMC142451, 25 Sept 1981, D.K. McAlpine); Richmond Rv (1, AMC142461, Cox coll); Port Stephens, on island in port (7, AMC63730, Oct 1892, ex Bland, ex Cox); Port Macquarie (4, AMC36565, ex Hedley); Col's Cave, Carrai S.F., in litter near entrance (1, AMC121693, 20 Feb 1980, P.H. Colman); Carrai Cave, Carrai S.F., in litter vine forest (8, AMC121701, 21 Feb 1980, P.H. Colman); Toonumbar Forest Road c. 34 km from Kyogle, Toonumbar S.F., CNVF (28°33'S, 152°45'E) (1, AMC128501, 15 Mar 1981, AM/QM - ABRS); Newell Falls, Dorrigo N.P. (30°24'S, 152°45'E) (1, AMC128337, 12 Mar 1981, ABRS - AM/QM); Acacia Plateau Road, c. 12.2 km from Acacia Ck-Killarney Road, Koreelah S.F., SEVT (28°21'S, 152°24'E) (3, AMC128562, QMMO10960, 15 Mar 1981, AM/QM - ABRS); Mt Warning N.P. (28°24'S, 153°16'E) (1, AMC129290, 18 Mar 1981, AM/QM - ABRS); Tooloom Scrub, Beaury S.F., NVF, (28°29'S, 152°24'E) (6, AMC128538, QMMO10941, 15 Mar 1981, AM/QM - ABRS); Wiangarie S.F., c. 25 km NE Kyogle, 1000 m (28°23'S, 153°06'E) (2, AMC142480, 17 May 1976, P.H. Colman, I. Loch); Koreelah Ck, Beaury S.F., c. 15 km W of Urbenville, 530 m (28°21'S, 152°20'E) (3, AMC142477, 18 May 1976, P.H. Colman, I. Loch); Cherry Tree North S.F., c. 40 km W of Casino, 400 m (28°54'S, 152°45'E) (24, AMC142478, 19 May 1976, P.H. Colman, I. Loch); Beaury S.F., c. 15 km W of Urbenville, 810 m (28°27'S, 152°24'E) (17, AMC142479, 18 May 1976, P.H. Colman, I. Loch); O'Donnell Ck, nr Eden Creek, 15 km N of Kyogle (1, AMC131453, 13 May 1981, N. Moulds, C. Smithers); Ourimbah Scrubs, nr Gosford (1, AMC152163, Oct 1904, S.W. Jackson); Newcastle (1, AMC152162, 1904, S.W. Jackson); Moonie Moonie Creek, nr Gosford (3, AMC142933, on tree trunk in rainforest, 6 Dec 1979, B. Day; 1, AMC142931, 26 Jan 1984, D. McAlpine); Wentworth Falls, Blue Mountains (2, AMC142938, 12 Oct 1965, D.K. McAlpine); Gibraltar Range (1, QMMO17256, 10 Nov 1980, G.B. Monteith; 2, QMMO17257, 10 Nov 1980, R. Raven); Booyong Scrub, via Lismore (28°49'S, 153°30'E) (1, QMMO6337, 14 May 1977, M.J. Bishop); Richmond Range S.F. (28°41'S, 152°44'E) NVF (17, QMMO6266, 19 Apr 1976, M.J. Bishop); Upper Wilson's Creek (28°32'S, 153°24'E), in litter (1, QMMO16791, 16 Nov 1983, AM/QM - ABRS); Bellingen River (30°27'S, 152°32'E), rainforest in gully (1, QMMO10835, Mar 1981, AM/QM - ABRS); Wentworth Falls (2, AMC26350, ex C. Laseron); Sherrard Falls, Dorrigo, 600 m, rainforest, in litter (1, QMMO16777, 13 Nov 1983, AM/QM - ABRS); Swans Rd, Bruxner Park Flora Reserve, litter, NVF (3, QMMO16783, 14 Nov 1983, AM/QM - ABRS); Whian Whian S.F., c. 7 km N of Dorroughby, NVF (1, QMMO16788, 15 Nov 1983, AM/QM - ABRS); Sea Acres Nature Reserve, Port Macquarie, littoral rainforest with palms (1, QMMO16793, 9 Dec 1983, P.H. Colman); Byrrill Creek Tributary, on Mebbin forest road (28°27'S, 153°12'E) (1, QMMO10407, Mar 1981, AM/QM - ABRS).

QUEENSLAND: Near monument, Cunningham Gap N.P., NVF (28°04'S, 152°24'E) (1, AMC128611, 16 Mar 1981, AM/QM-ABRS); Bunya Mountains N.P., (1, AMC142464, 8 Feb 1961, D.F. McMichael); Coolabunia pine scrubs, nr Kingaroy, on pine trunks (2, QMC 142460, Jun 1908, S.W. Jackson; 5, AMC142462, Jun 1908, ex Helms, S.W. Jackson); Little Nerang Creek (3, AMC55505, ex Brazier); Dandabah, Bunya Mts (26, AMC136617, QMMO12295, 31 Sept 1982, AM/QM-ABRS); Halls Plain, E of Emu Vale, CNVF, crawling on log (1, QMMO16898, 4 May 1986, J. Stanisic, J. Chaseling); Binna Burra, Lamington N.P., crawling on 'cordylines' (4, QM-MO14976, 10 Mar 1986, D.G. & N.G. Potter); Mt Hobwee, Lamington N.P. (28°13'S, 153°13'E), 1150 m, MFF, (1, QMMO6077, Apr 1976, M.J. Bishop); Toowoomba (27°34'S, 151°57'E) rainforest, (1, QM-MO6276, 25 Sept 1976, R. Raven); Dandabah, Bunya Mts (26°53'S, 151°35'E) Araucaria/NVF (90, QM-MO6068, FMNH 206312, 5 Mar 1976, M.J. Bishop); Upper Pine Creek, via Canungra, NVF/*Araucaria*, litter (2, QMMO16541, 1 Oct 1986, J. Stanisic, D. Potter); Tullawallal Circuit, Binna Burra, Lamington N.P., NVF, under logs (1, QMMO16736, 2 Oct 1985, J. Stanisic, D. Potter, J. Chaseling); Dandabah, Bunya Mts, behind picnic area (26°53'S, 151°36'E) (11, AM-C136617, 31 Sept 1982, AM/QM-ABRS).

DIAGNOSIS

Shell trochoid (Fig. 23c), diameter 6.22–10.08 mm (mean 7.77 mm) with 4 5/8–6 5/8 (mean 6 1/8+) normally coiled whorls, last whorl descending. Apex and spire strongly elevated, SP/BWW ratio 0.36-0.88 (mean 0.66), height 5.04–7.98 mm (mean 6.01 mm), H/D ratio 0.71–0.88 (mean 0.78). Protoconch of 1 1/2–1 5/8 whorls, mean diameter 875.0μm at 1 1/2 whorls. Apical sculpture of irregular pits and vague radial rugosities (Fig. 23e). Postnuclear sculpture of low spiral thickenings crossed by numerous low protractively sinuated radial ribs in a reticulate pattern (Fig. 23f), becoming less pronounced after the first four whorls (Fig. 23a). Sculpture continued on the base but reduced (Fig. 23b). No additional microsculpture. Umbilicus small, diameter 0.62–1.54 mm (mean 0.89) D/U ratio 6.55–11.28 (mean 9.01), partially obscured by the reflected columella. Sutures lightly impressed. Whorls rounded above and below a strongly angulate to thread-carinate periphery. Aperture ovately lunate. Lip simple, columella dilated and reflected over the umbilicus. Parietal callus well developed. Periostracum strongly deciduous. Colour (with periostracum) creamy-yellow; (without) whitish-pink, often with a darker brown to pink apex and spire. Based on 20 measured adults.

Genitalia with epiphallus (Fig. 24b) reflexing before entering the penis apically through a fleshy pilaster (Fig. 24c). Penial retractor muscle inserting adjacent to the penis/epiphallus junction. Penis (Fig. 24c) long and slender, muscular, with an apical bulb containing a grooved, muscular thickening. Penis proper with spongy longitudinal pilasters. Free oviduct thick, muscularised, longer than vagina (Fig. 24a). Vagina short, internally with longitudinal pilasters.

Radula (Fig. 23g, h) with tricuspid central and lateral teeth which have long lanceolate mesocones and well developed anterior flares.

Based on 6 dissected specimens (QM-MO6068, FMNH206312).

RANGE AND HABITAT

H. delta inhabits cool subtropical notophyll vine forests of the Great Dividing Range from Dorrigo, NSW to the Bunya Mountains, SEQ; the humid warm notophyll vine forests of the coastal region of northern NSW; warm temperate rainforests in the Gosford and Blue Mountains area of central NSW; and some marginally drier subtropical forest (microphyll vine forest, semi-evergreen vine thicket) in southern Queensland. The distribution of *H. delta* at the southern end of its range is not well known.

REMARKS

H. delta has a caudal horn. This structure is typical of some New Zealand arboreal charopids and is common in Australian helicarionids.

The shell of *H. delta* has an apical portion of about 4 whorls in which the sculptural features are quite prominent, but on the remaining whorls sculpture is almost absent. A similar pattern is seen in *H. ailaketoae*. This is not gerontic growth and its significance, if any, is unknown.

Hedleyoconcha ailaketoae sp. nov.
(Fig. 26a–e; Tables 2, 6)

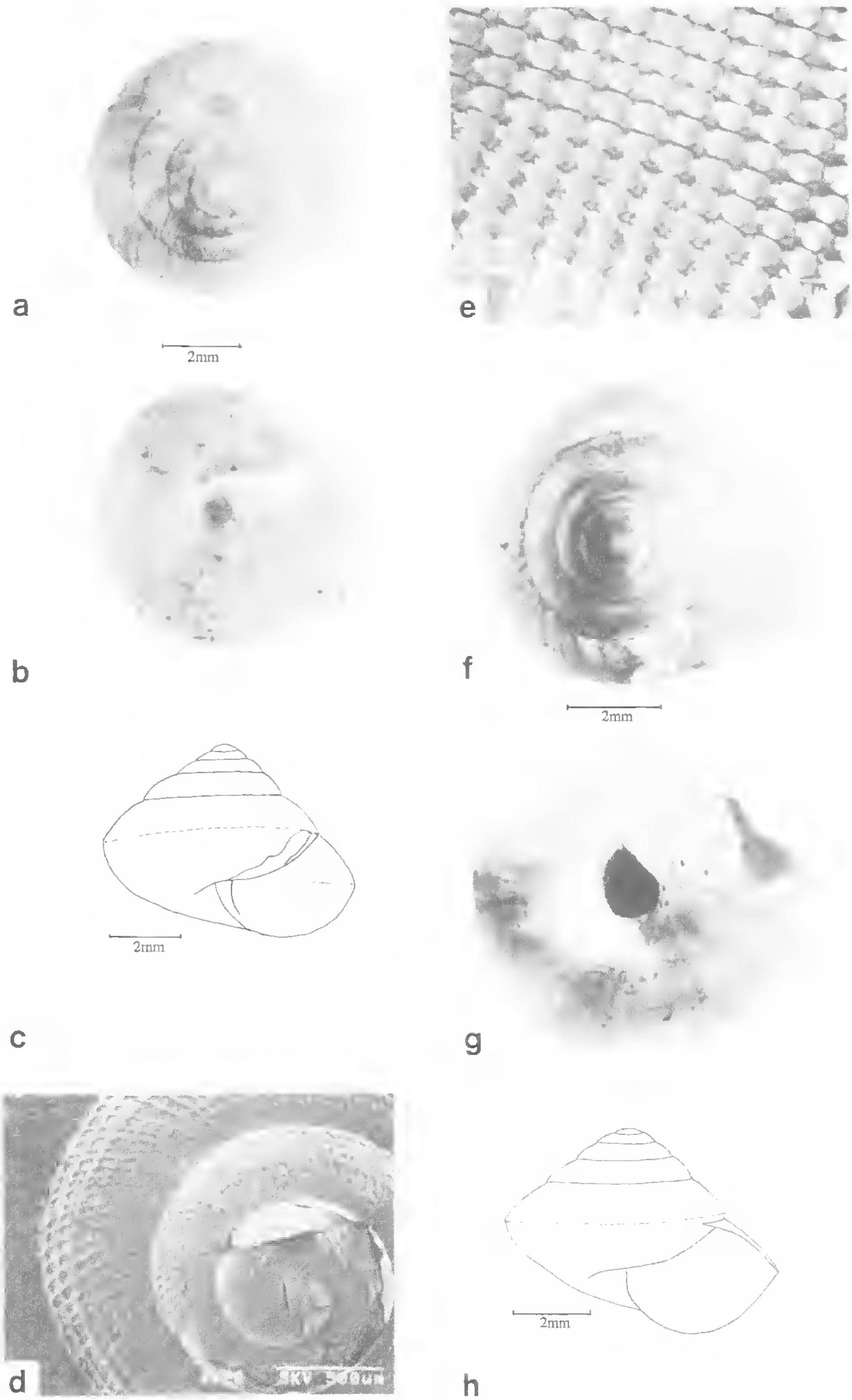
ETYMOLOGY

For Dr Aila Keto in recognition of her efforts for rainforest conservation.

COMPARISONS

H. ailaketoae is distinguished from *H. delta* by its smaller size, fewer whorls, less elevated shell, weaker apical sculpture, and more prominent reticulate sculpture on postnuclear whorls (Fig. 26a–d). The sympatric *Oreokera cumulus* (Odhner, 1917) has an elevated, keeled shell but is larger, has fewer whorls, apical spiral cords,

FIG. 26. a–e. *Hedleyoconcha ailaketoae* sp.nov. a-c, Summit, Mt. Bellenden Ker, NEQ, QMMO11254, holotype; d–e, Mt. Bellenden Ker, NEQ, QMMO15802, QMMO11273, paratypes. a-c, whole shell; d, apical-postapical sculpture; e, central and lateral teeth. f-h, *Hedleyoconcha addita* Iredale, 1944, AMC63488, lectotype.


a
e
2mm
b
f
2mm
2mm
c
g
d
5KV
h
2mm

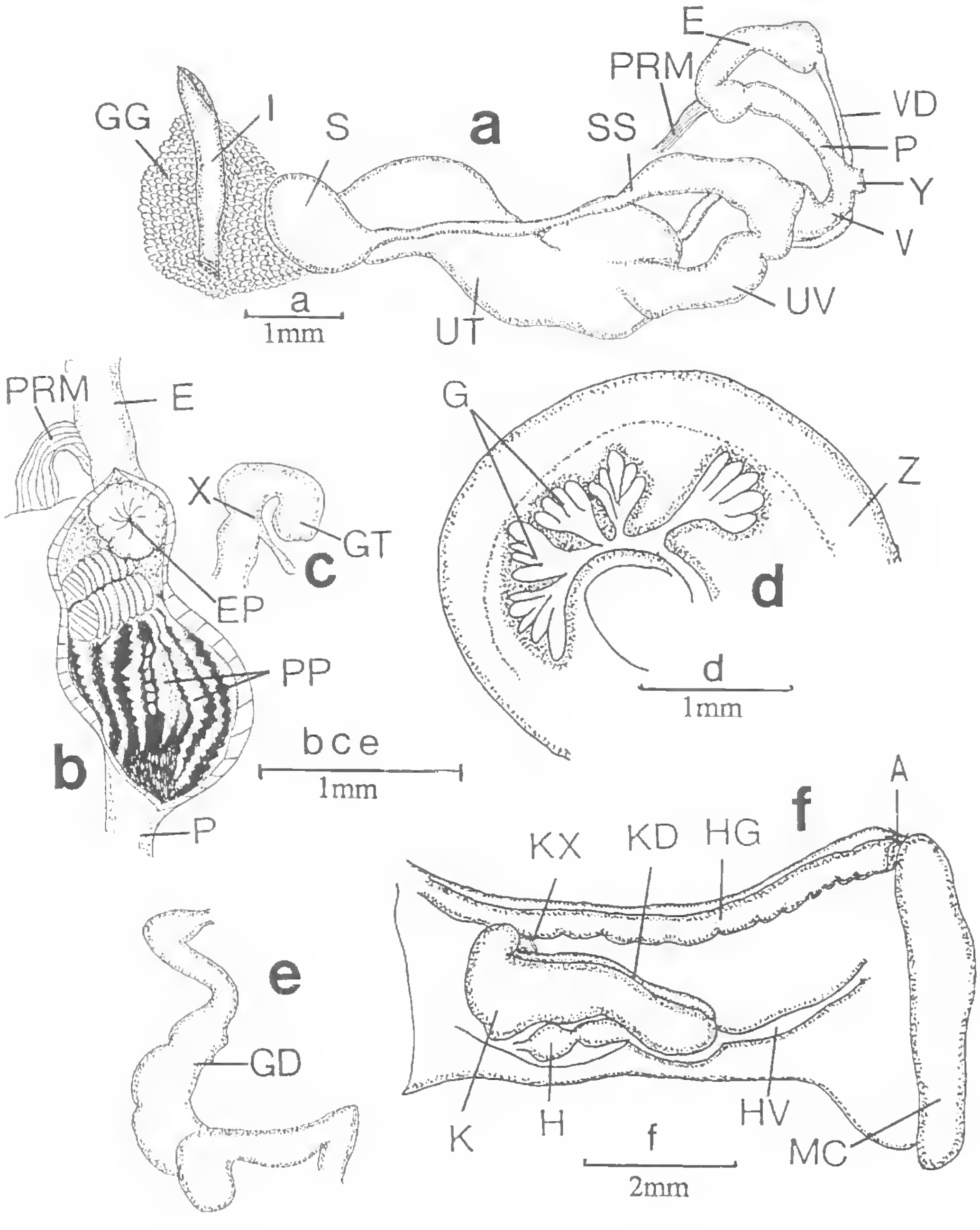


FIG. 27. *Hedleyoconcha ailaketoae* sp.nov. Mt. Bellenden Ker, NEQ. QMMO15802, paratype. a, genitalia; b, details of penis interior; c, talon; d, ovotestis; e, hermaphroditic duct; f, pallial cavity.

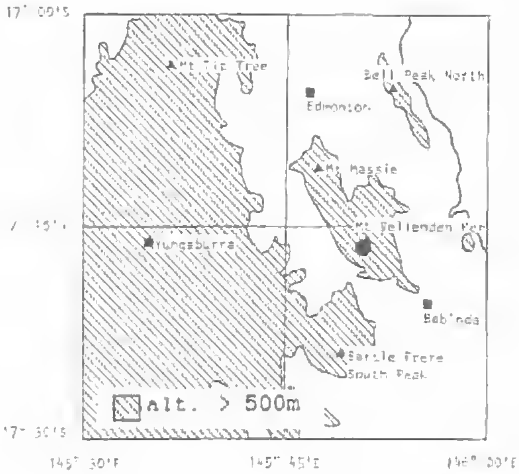


FIG. 28. Distribution of *Hedleyoconcha ailaketoae* sp. nov.

and postnuclear sculpture of prominent radial ribs with reticulate microsculpture (Stanisic, 1987, pls 1,2).

TYPE MATERIAL

HOLOTYPE: QMMO11254, Mt Bellenden Ker, NEQ. Summit, 1560 m, SMVFT. Collected Earthwatch/QM, 17–24 Oct 1981. Height of shell 5.13 mm, diameter 6.81 mm, H/D ratio 0.75, D/U ratio 9.47, whorls 5 1/8+.

PARATYPES: Mt Bellenden Ker, NEQ. Summit TV stn, 1560 m (17°16'S, 145°51'E) rainforest (2, QMMO15802, 29 Apr 1983, G.B. Monteith, D. Yeates); Mt Bellenden Ker, NEQ. summit, 1560 m, SMVFT (1, QMMO11273, 1–7 Nov 1981, Earthwatch/QM).

DIAGNOSIS

Shell trochoid (Fig. 26c), diameter 5.97-6.81 mm (mean 6.39 mm) with 5 1/8 normally coiled whorls. Apex and spire strongly elevated, SP/BWW ratio 0.54-0.63 (mean 0.61), height 4.62-6.13 mm (mean 4.88 mm). H/D ratio 0.75–0.77 (mean 0.76). Protoconch 1 1/2 normally coiled whorls, mean diameter 965μm at 1 1/2 whorls. Apical sculpture of weak irregular pits (Fig. 26d). Postnuclear sculpture of prominent, spiral cords crossed by crowded, protractively sinuated radial ribs in a strongly reticulate pattern which becomes less pronounced after c. 4 whorls (Fig. 26b). Sculpture continuous on the base but somewhat reduced. No additional microsculpture. Umbilicus very small, diameter 0.72 mm, D/U ratio 8.30–9.47 (mean 8.89), partially covered by columella. Sutures lightly impressed. Whorls rounded above and below a thread-carinate periphery. Aperture ovately lunate. Lip simple, columella dilated and reflected over the umbilicus. Parietal callus well-developed. Periostracum deciduous. Colour (with periostracum) straw yellow, spire darker. Based on 2 measured adults.

Epiphallus (Fig. 27a) long, entering penis apically through a fleshy circular pad. Penis (Fig. 27b) shorter than epiphallus, slender with corrugated, longitudinal pilasters (Fig. 27b), apically with a penial bulb containing entrance of epiphallus (Fig. 27b) and a muscular grooved collar. Penial retractor muscle inserted at the penial bulb/epiphallus junction. Free oviduct muscularised, much longer than vagina (Fig. 27a). Vagina short with longitudinal pilasters internally.

Radula (Fig. 23e) with tricuspid central and lateral teeth which have long mesocones and strongly developed anterior flares. No data available on marginal teeth.

Based on 1 dissected adult (QMMO15802).

RANGE AND HABITAT

H. ailaketoae has only been found to date in simple microphyll vine fern thickets and forests on the summit of Mt. Bellenden Ker, NEQ. Its microhabitat is unknown.

REMARKS

Discovery of *H. ailaketoae* on Mt. Bellenden Ker was unusual considering that its nearest relative is almost 1400 km to the south. Previously Stanisic (1987) reported on the altitudinally restricted charopids from this region.

Hedleyoconcha addita Iredale, 1944

(Fig. 26f–h; Tables 2, 6)

Hedleyoconcha addita Iredale, 1944, p. 317, pl. 19, fig. 19

COMPARISONS

In general appearance, *H. addita* bears some resemblance to *H. delta*. The two type specimens are worn and only a few traces of vaguely reticulate adult sculpture are visible. However, reticulate postnuclear sculpture is not sufficient to conclusively link this species with the two mainland congeners. The keel of *H. addita* is much more pronounced than in either *H. delta* or *H. ailaketoae* and may indicate that the overall similarity of *H. addita* to these species is convergent, but in the absence of other evidence, the original allocation of Iredale (1944) is retained.

TYPE MATERIAL

LECTOTYPE: AMC63488. Mt Gower, SSE, Lord Howe Island.

PARALECTOTYPE. AMC150093, same collection data as lectotype.

DIAGNOSIS

Shell moderately large, trochoid (Fig. 26g), diameter 6.89–6.98 mm (mean 6.94 mm) with 6 to 6 1/8 (mean 6+) normally coiled whorls, the last whorl descending slightly. Apex and spire strongly elevated, SP/BWW ratio 0.63–0.67 (mean 0.65), height 5.38–5.46 mm (mean 5.42 mm). H/D ratio 0.77–0.79 (mean 0.78). Protoconch of 1 3/4 whorls, mean diameter 882.5μm at 1 1/2 whorls. Apical sculpture worn on available specimens. Post nuclear sculpture also mostly worn. Body whorl with remnant patches of periostracum and sculpture consisting of low crowded spiral cords and weak protractively sinuated radial growth ridges. Sculpture continuous on the base as crowded spiral cords and weak protractively sinuated radial growth ridges (Fig. 26g). No additional microsculpture visible. Umbilicus narrow, V-shaped, only slightly covered by the columella (Fig. 26h), diameter 1.48–1.54 mm (mean 1.51 mm). D/U ratio 4.53–4.66 (mean 4.60). Sutures only slightly impressed. Whorls rounded above and below a strongly carinate periphery. Aperture quadrate to roundly lunate. Lip simple, columella dilated and partially reflected over the umbilicus. Parietal callus developed. Periostracum deciduous. Colour (with periostracum) straw yellow, (without periostracum) chalky whitish-pink, with a darker spire. Based on 2 measured adults.

Anatomy unknown.

Lenwebbia gen. nov.

ETYMOLOGY

For Dr Len Webb in recognition of his pioneering studies on rainforest evolution.

TYPE SPECIES

Lenwebbia protoscrobiculata sp. nov.

DIAGNOSIS

Shell small, moderately elevated (Fig. 29c) average diameter 4.35 mm and relatively few (average 4 1/8+) rounded whorls. Protoconch sculpture of numerous dimples and vague radial ridges (Fig. 29g). Adult sculpture of spiral grooves, broad radial undulations and very fine thread-like radial ribs (Fig. 29e,f). Base with incised spiral lines and weak, raised radial growth lines. Sutures impressed. Umbilicus small (Fig. 29b). Lip simple, columella dilated and deflected toward the umbilicus.

Foot and tail broad, bluntly tapering posteriorly. No caudal horn or foss. Body colour (in preservative) grey. Ommatophores black. Pallial roof with some black speckling. Kidney orange, triangular, c. 1/2 length of the pallial cavity. Rectal kidney lobe reduced. Ureter sigmurethrous with an incomplete secondary arm and reflexed primary arm (Fig. 30c). Ureteric opening located at the rear of the pallial cavity in the angle between the kidney and the hindgut. Ovotestis (Fig. 30c) several clumps of palmately clavate lobes of alveoli, oriented at right angles to the plane of coiling. Terminal male genitalia with short muscular epiphallus (Fig. 30b) entering penis apically through a simple pore (Fig. 30b). Penis elongate, internally with few, large longitudinal pilasters (Fig. 30b). Free oviduct (Fig. 30a) longer than vagina, otherwise typical. Radula (Fig. 29d) with mesocone of central and lateral teeth long, lanceolate. Marginal teeth typical.

COMPARISONS

Lenwebbia differs from *Ngairea* in its smaller size, more weakly sculptured shell and more strongly pitted apex (Fig. 29g). Anatomically, the reflexed primary ureter (Fig. 30e) and brightly coloured kidney of *Lenwebbia* are distinctive. In the Mudlo Gap area, SEQ, *Lenwebbia* is sympatric with *Coenocharopa* whose worn shells are grossly similar. However *Coenocharopa* has an apex with curved radials and raised spiral cords (Figs 111f, 114f, 120f–h), adult sculpture of fine radials and spiral cords (Figs 111g, 114g, 120d), and more shouldered whorls. The sympatric helicarionid *Tarocystis* Iredale, 1937, has a protoconch with incised spiral lines and adult sculpture of incised spiral grooves which have regular notches along their length.

Lenwebbia protoscrobiculata sp. nov.
(Figs 29-31; Tables 2, 7)

ETYMOLOGY

Latin *scrobiculus*, a little ditch; for the punctate protoconch.

TABLE 7. LOCAL VARIATION IN *LENWEBBIA PROTOSCROBICULATA* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Lenwebbia protoscrobiculata Kalpowar S.F. QMMO 17048 (Holotype)	1	4 3/8	2.94	4.49	0.63	0.60	2.34	0.25	--	--	0.82	5.71
QMMO 17047	10	4 1/4 (4 1/8 to 4 3/8+)	2.88±0.077 (2.64–3.15)	4.47±0.056 (4.17–4.69)	0.64±0.007 (0.61–0.67)	0.46±0.018 (0.38–0.55)	2.40±0.038 (2.26–2.68)	0.20±0.008 (0.16–0.24)	--	--	0.75±0.016 (0.72–0.82)	5.98±0.126 (5.45–6.52)
Dawes Range QMMO 12652	1	4 2/8+	2.98	4.47	0.67	0.60	2.39	0.25	--	--	0.76	5.88
Mt Woowoonga QMMO 12447	1	4 1/8+	2.64	4.05	0.65	0.38	2.26	0.17		--	0.74	5.47
Clifton Range QMMO 12386	1	4 3/8+	3.11	4.39	0.71	0.68	2.43	0.28		--	0.82	5.34
Mt Mudlo QMMO 8359	10	4+ (3 7/8–4 1/4)	2.69±0.032 (2.56–2.81)	4.20±0.038 (3.96–4.34)	0.64±0.007 (0.61–0.67)	0.40±0.022 (0.30–0.47)	2.29±0.030 (2.13–2.43)	0.17±0.011 (0.12–0.21)			0.73±0.013 (0.62–0.76)	5.81±0.086 (5.38–6.43)

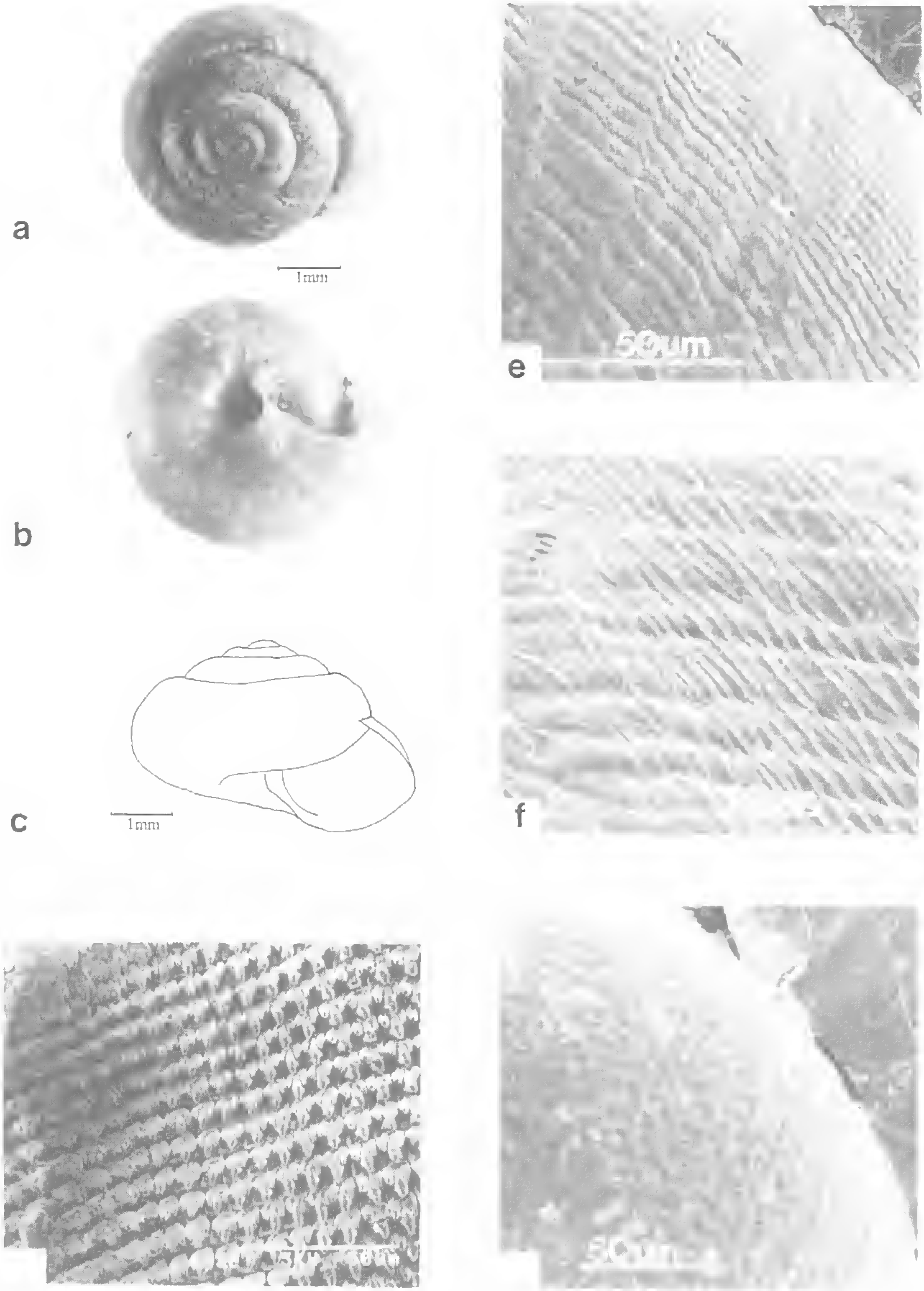
Comparisons

L. protoscrobiculata most closely resembles *Ngairea canaliculata* which is sympatric with the former in the northern parts of its range. *N. canaliculata* lacks the punctate protoconch of *L. protoscrobiculata*, has prominent post nuclear radial ribs (Fig. 12a), channelled sutures (Fig. 12e) and flammulated shell. In the southern part of its range *L. protoscrobiculata* is sympatric with *Coenocharopa macromphala* and *C. parvicostata* and may be confused with worn dead shells of these latter two species. However *Coenocharopa* has apical sculpture of curved radial ribs and low spiral cords and is smaller (Figs 114e-g; 120d-h). Anatomically a complete secondary ureter (Figs 115a, 121a) is sufficient to distinguish these species from *L. protoscrobiculata*.

Type Material

Holotype: QMMO17048, c. 8 km from Kalpowar on Fireclay Rd, Kalpowar S.F., SEQ (24°43'S, 151°21'E) leaf litter, MVF/*Araucaria*. Collected by J. Stanisic, A. Green, 15 July 1980. Height of shell 2.94 mm, diameter 4.49mm, H/D ratio 0.63, D/U ratio 5.71, whorls 4 3/8.

Paratypes: SOUTH EAST QUEENSLAND - QMMO17047, same data as holotype, 36 specimens; Mt Mudlo, Kilkivan S.F. (26°01'S, 152°13'E) leaf litter, NVF/Araucaria (34, QMMO8359, 17 Jul 1980, J. Stanisic, A. Green); Mudlo Gap, Kilkivan S.F., litter MVF/Araucaria (3, QMMO16843, 5 Jul 1984, J. Stanisic, D. Potter, K.Emberton); Mudlo Gap S.F. (26°01'S, 152°14'E) MVF/*Araucaria* (7, QMMO12365, AMC13665, 2 Sept 1982, AM/QM-ABRS); Clifton Range S.F., SW of Fairlies Knob, *Araucaria*/MVF (26°34'S, 152°16'E) (2, QMMO-12386, AMC136681, 2 Sept 1982, AM/QM-ABRS); Dawes Range, MVF/Araucaria (24°28'S, 151°07'E) (2, QMMO12652, 4 Sept 1982, AM/QM-ABRS); c. 4 km below summit of Mt Fort William on Mt Fort William Rd, Kalpowar S.F., litter, under rocks, logs, MVF/*Araucaria* (7, QMMO17010, QMMO16839, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton); rainforest walk, Kalpowar S.F. (24°41'S, 151°21'E) MVF/*Araucaria* (1, QMMO12578, 4 Sept 1982, AM/QM-ABRS); base of Mt Woowoonga, (25°26'S, 152°06'E) MVF/*Araucaria* (5, QMMO12447, AMC136720, 3 Sept 1982, QM/QM-ABRS); Mt Goonaneman, via Childers, rainforest, 670 m, litter (2, QMMO17258, 3-7 Nov 1980, R. Raven, V. Davies); Mt Goonaneman, rainforest (2, QMMO17259, 6 Feb 1981, G.B. Monteith); Mt Colosseum, 6 mls S of Miriam Vale (12, AMC142928, 6 Jun 1964, L. Price); Kalpowar S.F., NE of Monto, SEQ (24°42'S,


a
1mm
b
c
1mm
e
50um
f
50um

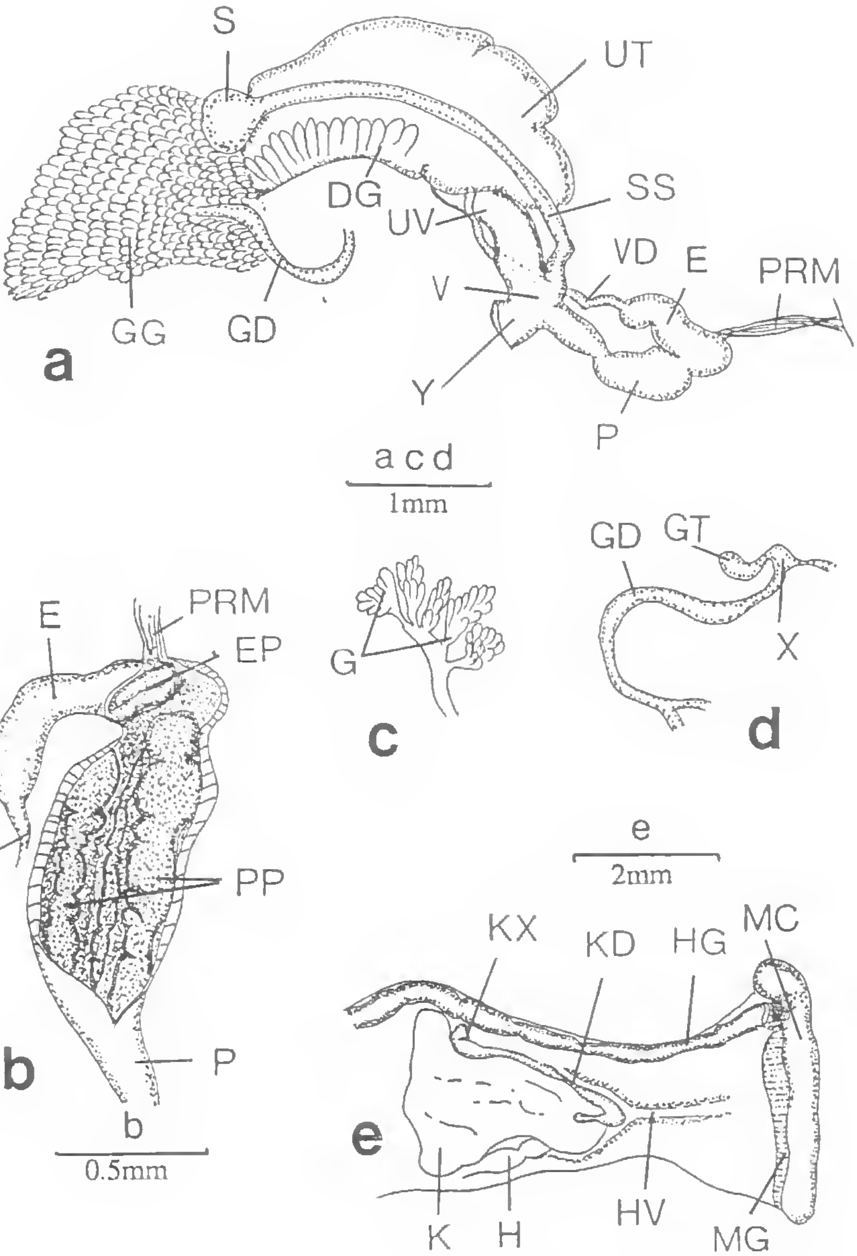


FIG. 30. *Lenwebbia protoscrobiculata* sp. nov. c. 4km below summit of Mt. Fort William on Mt. Fort William Rd, Kalpowar S.F., SEQ. QMMO17010, paratype. a, genitalia; b, details of penis interior; c, structure of ovotestis; d, details of hermaphroditic duct and talon; e, pallial cavity. Scale lines as marked.

FIG. 29. *Lenwebbia protoscrobiculata* sp.nov. a–c, c. 8km from Kalpowar on Fireclay Rd, Kalpowar S.F., SEQ. QMMO17048, holotype; d, Summit of Mt Fort William, Kalpowar S.F., SEQ. QMMO17010, paratype; e–g, Mt Mudlo, Kilkivan S.F., SEQ. QMMO8359, paratype. a–c, entire shell; d, lateral and marginal teeth; e, early post nuclear sculpture; f, late postnuclear sculpture; g, apical sculpture. Scale lines as marked.

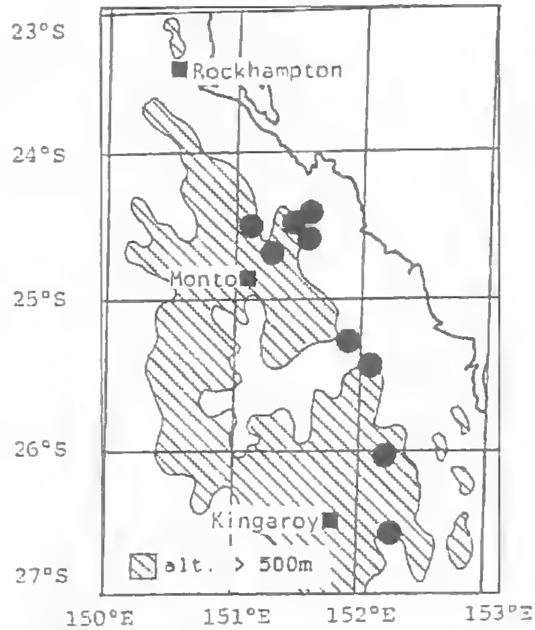


FIG. 31. Distribution of *Lenwebbia protoscrobiculata* sp. nov.

151°21'E) vine thicket/scrub (8, QMMO13146, 4 Sept 1982, AM/QM-ABRS); Camp Creek, SW side of Bobby Range, S of Miriam Vale, SEQ (24°36'20"S, 151°33'E) (1, QMMO13287, 6 Sept 1982, AM/QM-ABRS); Limestone Ck, W. of Childers, SEQ (25°15'30"S, 151°55'E) (2, QMMO13009, 3 Sept 1982, AM/QM-ABRS).

OTHER MATERIAL

SOUTH-EAST QUEENSLAND: Bulburin S.F. (24°32'S, 151°29'E) rainforest (1, QMMO17260, 8 Mar 1977, QM party); summit Mt Booroon Booroon, SW of Miriam Vale, MVF/*Araucaria*, litter (1, QMMO16861, 17 Sept 1985, J. Stanisic, D. Potter); Dawes Range, MVF/*Araucaria* (24°28'S, 151°07'E) (1, AMC136781, 4 Sept 1982, AM/QM-ABRS).

DIAGNOSIS

Shell small, depressed, diameter 3.96–4.69 mm (mean 4.35 mm) with 3 7/8 to 4 3/8 (mean 4 1/8+) normally coiled whorls. Last whorl descending only very slightly. Apex and spire elevated (Fig. 29c), SP/BWW ratio 0.12–0.28 (mean 0.19) height 2.56–3.15 mm (mean 2.79 mm). H/D ratio 0.61–0.71 (mean 0.64). Apical sculpture highly modified, consisting of numerous, crowded dimples with a few, vague, radial ridges mainly at the terminal portion of the protoconch (Fig. 29g). Protoconch of 1 1/2 to 1 1/2+ whorls, mean diameter 906.9μm at 1 1/2 whorls. Post nuclear sculpture of spiral grooves, closely spaced, occasionally interrupted and crossed by weakly protractively sinuated radial ridges (Fig. 29e). Secondary sculpture of fine, crowded, radial growth ridges particularly on the body whorl (Fig. 29f). Umbilicus small, barely covered by the reflection of the columella, diameter 0.62–0.82 mm (mean 0.75 mm), D/U ratio 5.34–6.52 (mean 5.85 mm). Sutures impressed. Whorls rounded. Aperture roundly lunate. Lip simple, columella dilated, slightly thickened and deflected toward the umbilicus. Parietal callus not strongly developed. Base glossy, rounded, with a sculpture of incised spiral striae and weak radial growth lines. Colour yellow-brown with a darker, grey spire in some specimens. Based on 24 measured adults.

Genitalia with epiphallus entering the penis through a simple pore (Fig. 30b), internally with longitudinal pilasters. Penis a muscular tube with spongy longitudinal pilasters (Fig. 30b). Penial retractor muscle inserting at the penis/epiphallus junction. Free oviduct (Fig. 30a) a long, thickened muscular tube, internally with longitudinal thickenings.

Radula (Fig. 29d) with tricuspid central and lateral teeth in which the mesocone is long and lanceolate.

Based on 3 dissected adults (QMMO17010, AMC142928).

RANGE AND HABITAT

L. protoscrobiculata inhabits the drier subtropical microphyll vine forests (with *Araucaria* emergents) between Mudlo Gap and Bobby Range, SEQ, and rarely, moister subtropical notophyll vine forests where these are in juxtaposition with drier rainforest. Little is known about the microhabitat of *L. protoscrobiculata* because most available material consists of dead shells collected from litter. However, some live specimens have been taken from the upper surface of rotting logs. The comparatively reduced sculpture of *L. protoscrobiculata* is not indicative of life under logs but rather suggests that the species lives in curled leaves, or under bark of trees.

REMARKS

At first glance *L. protoscrobiculata* appears more like a helicarionid than a charopid. Reduced radial sculpture (Fig. 29a), shell colour, and coiling pattern are not typically charopid. However the peculiar apical sculpture (Fig. 29g), reticulate adult microsculpture (Fig. 29f) and anatomy (Fig. 30), leave no doubts about its true affinities.

The incomplete secondary ureter (Fig. 30e) is inconsistent with living in drier habitats but in the case of *L. protoscrobiculata* the primary ureter is lengthened by reflexion at the kidney apex.

L. protoscrobiculata appears to be a derivative of the *Ngairea* group. The distinctive punctate apex, incised spiral grooves on the post nuclear shell and coiling pattern of reduced number of rounded whorls can all be readily derived from *Ngairea*. Anatomically, the differences from *Ngairea* are not great.

Setomedea Iredale, 1941

Setomedea Iredale, 1933, p. 53 nom. nud.; Iredale, 1937a, p. 329, nom. nud.; Iredale 1941a, p. 267; Iredale, 1941b, p. 1; Burch, 1976, p. 133.
Setomedia (error) Kershaw, 1956b, p. 7.

TYPE SPECIES

Suteria seticostata Hedley, 1924; by original designation.

PREVIOUS STUDIES

Iredale (1933) introduced *Setomedea* for *Suteria seticostata* Hedley, 1924 without any accompanying description. Subsequently Iredale (1941a, p. 267) provided a barely minimal description and I consider that the name should date from that publication. Iredale (1937a, p. 329) included *'Endodonta' aculeata* Hedley, 1899 from Wollongong, NSW without giving reasons. *Setomedea*, herein, includes *S. seticostata*, three new species from Queensland, and a possible new species from the Atherton Tableland. *'Endodonta' aculeata* Hedley, 1899 is excluded to be dealt with later.

DIAGNOSIS

Small to medium sized Charopidae, adult shell diameter 2.56-5.71 mm, with 3 5/8 to 5 5/8+ normally to loosely (*nudicostata*) coiled whorls. Height of shell 1.36-3.37 mm. Apex and spire slightly (*seticostata*) to strongly (*monteithi*) elevated. Body whorl descending in front. Protoconch shiny, rounded, with 1 3/8 to 1 5/8+ whorls. Apical sculpture of numerous slightly (*seticostata*, *janae*) to strongly (*nudicostata*, *monteithi*) squiggly spiral cords with a few vague radial undulations mainly near the end of the protoconch. Postnuclear sculpture complex, of broad spiral furrows (except in *nudicostata*) and numerous, moderately spaced, complex radial ribs formed by the enlargement of 2–3 radial riblets. The major ribs have periostracal blades scalloped (caused by the spiral undulations in the shell surface) or normal (*nudicostata*), with or without (*nudicostata*) regularly spaced slender setae along their length. Microsculpture of fine, crowded radial riblets, 7–15 between each pair of major ribs, and numerous, crowded spiral cords on the radial ribs. Sculpture continuous on the base. Umbilicus wide U-shaped to narrow V-shaped (*nudicostata*). Sutures impressed. Whorls shouldered above and rounded below a slightly compressed periphery, or rounded above and flattened at the basal margins (*nudicostata*). Aperture roundly lunate. Lip simple, columella slightly thickened. Parietal callus developed. Colour yellow-horn to browny-yellow with reddish-brown flammulations and suffusions.

Foot short and broad, bluntly tapered posteriorly. No caudal horn or foss developed. Colour of animal (in preservative) creamy; dark in *nudicostata*. Ommatophores (in preservative) black (*seticostata*, *nudicostata*) or white (*janae*, *monteithi*). Kidney broadly triangular to elongate. Ureter sigmurethrous. Secondary ureter incomplete with ureteric opening at rear of the pallial cavity adjacent to the hindgut. Initial part of the primary ureter reflexed and coiled about the kidney apex. Ovotestis two clumps of palmately clavate lobes of alveoli located in the apical whorls of the digestive gland or above the stomach (*nudicostata*), oriented parallel to the plane of coiling.

Terminal male genitalia with a muscularised epiphallus which may be short (*monteithi*), moderately long, very long (*nudicostata*), or modified and partially incorporated into the penial apex (*janae*). Epiphallic pore simple, entering bulb of penis apically or subapically (*seticostata*, *monteithi*), or entering directly into lower penial chamber (*janae*). Penial retractor muscle inserting on the penial apex (*monteithi*), on the epiphallus near the penial bulb, or on the epiphallus well removed from the penis (*nudicostata*). Penis with an apical bulb separated from the main penial chamber by a muscular collar, or without a muscular collar (*nudicostata*). Apical bulb with pilasters (*monteithi*, *seticostata*), verge (*nudicostata*) or with incorporated epiphallus (*janae*). Penis proper with fleshy, longitudinal pilasters or low longitudinal pustular thickenings (*nudicostata*).

Radula with tricuspid central tooth that has a

TABLE 8 - RANGE OF VARIATION IN *SETOMEDEA* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Setomedea setcostata	13	5- (4 5/8-5 1/4)	2 05 (1 75-2.34)	3.91 (3 41-4.47)	0.52 (0.47-0 59)	0 25 (0.17-0.30)	1.23 (1.15–1.32)	0.20 (0.14–0.24)	72.57 (61–94)	6.15 (5.42–7.16)	1.32 (1.15–1.54)	2.98 (2.81–3.13)
Setomedea junae	7	4 5/8- (4 1/2-to 4 3/4)	1 87 (1 66–2.08)	3.63 (3.41–3.71)	0.51 (0.49–0.58)	0.15 (0.04–0.21)	1.22 (1.15–1.28)	0.12 (0.04–0.17)	59.67 (49–80)	5.22 (4.57–6.87)	1.18 (1.01–1.31)	3.11 (2.68–3.68)
Setomedea monteithi	19	5 1/4- (4 1/2–5 5/8+)	2 78 (2.04–3 37)	4.60 0.61 (3.62–5.71)	0.42 (0.50–0.83)	1.59 (0.09–0.60)	0.26 (1.24–1.83)	71.50 (0.05–0.36)	4.91 (50–107)	1.36 (4.12–6.71)	3.41 (0.92–1.85)	(3.04–3.92)
Setomedea nudicostata	4	3 7/8+ (3 5/8-to 4 1/4)	1 55 (1 36–1 70)	2.86 (2.56–3.11)	0.55 (0.51–0.57)	0 24 (0.17–0.30)	0 89 (0.81–0.98)	0.27 (0.21–0.32)	80 (70–89)	8.92 (8.30–9.33)	0.83 (0.72–0.97)	3.44 (3.22–3.55)

slender, lanceolate mesocone and smaller pointed ectocones. Otherwise typical.

Distribution and Ecology

Setomedea has a disjunct distribution from Dorrigo, NSW, to Shiptons Flat, near Cooktown, north Queensland. It inhabits moist temperate and subtropical rainforests of northern NSW and southern Queensland, subtropical forests of the Mackay/Prosperine area, and humid tropical forests of north Queensland between Tully and Cooktown.

Setomedea lives under and in logs and occasionally may be found under bark with *Ngairea*. Species show a preference for very moist habitat where decomposition is well advanced. Large numbers of individuals can be found under the same log or piece of bark.

Patterns of Shell Variation

The umbilicus is typically wide U-shaped. Departures from this pattern are seen in *S. nudicostata* (Fig. 35b) from SEQ and *Setomedea* sp. (Fig. 44b) from the Atherton Tableland, north Queensland.

Variation in postnuclear sculptureis small. The most dramatic change is the loss of periostracal setae and spiral furrows in *Setomedea nudicostata* (Fig. 35f).

Periostracal setae are rare among the Charopidae and only a small number of Australian and New Zealand taxa posses them. On their own they do not indicate phylogenetic relationship. However in the case of *Setomedea*, anatomical patterns unite the group, and indicate that this character was derived from a common ancestor.

Patterns of Anatomical Variation

The incomplete secondary ureter of *Setomedea* is similar to that found in *Oreokera*, *Hedleyoconcha*, *Mussonula*, *Lenwebbia* and *Ngairea*. However, the apical region of the kidney has the pericardial lobe well developed (Fig. 36e). The initial section of the ureter is reflexed and coiled around the tip of the kidney giving the kidney apex an S-shaped appearance. While some genera (e.g. *Lenwebbia*), may have the initial part of the ureter reflexed, only *Setomedea* has this unusual coiling.

The terminal male genitalia of *Setomedea* show variations in the internal structures of the penis, shape and size of the epiphallus, and the insertion of the penial retractor muscle. Typically the epiphallus is a short, reflexed, muscular tube entering the penis either apically or subapically (Figs 42a. 33b). In *S. janae* part of the epiphallus is incorporated into the penial complex (Fig. 39c) and may represent spatial adjustment in response to reduced whorl count.

The apical and female genitalia of *Setomedea* are without unusual features except in *S. nudicostata* which has the free oviduct very long and the ovotestis situated in the digestive gland just above the level of the stomach. The shift in position of the ovotestis from apicad in the digestive gland is probably related to reduced whorl count.

COMPARISONS

Setomedea can be distinguished from other subtropical and tropical charopids with spirally lirate protoconchs by size, shell colour, and adult sculpture - *Oreokera* has a much larger trochoid shell (Stanisic, 1987, pls 1,2); *Sinployea* has a smaller, monochrome brown shell with more numerous, simple, radial ribs (Fig. 137a, e); and *Omphaloropa* is smaller in size, has broader apical cords, wide cup-shaped umbilicus and few, widely separate major ribs on the body whorl (Fig. 134a,b,e).

KEY TO SPECIES OF *SETOMEDEA*

1.Shell with periostracal setae 2

Shell without periostracal setae (Fig. 35a. f) .... *nudicostata*

2.Shell with looser coiling (Fig. 44a); fewer whorls (Fig. 44a); mean whorl count 3 7/8+ (Table 8) ....*Setomedea* sp.

Shell with tighter coiling; many whorls; mean whorl count greater than 4 1/2 3

3.Apical sculpture of regular spiral cords 4

Apical sculpture of squiggly spiral cords (Fig. 41e)...................................... *monteithi*

4.Major ribs with simple periostracal blades (Fig. 32f) .... *seticostata*

Major ribs with scalloped periostracal blades (Fig. 38g) .... *janae*

Setomedea seticostata (Hedley, 1924)
(Figs 32–34; Tables 8. 9)

Suteria seticostata Hedley, 1924, p. 221, pl. 32, figs. 41-44 .
Setomedea seticostata (Hedley): Iredale. 1937a, p. 329: Iredale, 1941a, p. 268, fig. 6; Iredale, 1941b, p. 1.
Setomedia (sic) seticostata (Hedley); Kershaw, 1956b, p. 7.

COMPARISONS

S. seticostata is characterised by a flammulated shell with spirally corded protoconch and adult sculpture of complex radial ribs, microspiral cords, microradials, spiral grooves and prominent periostracal setae. *S. janae* has fewer whorls with strongly scalloped periostracal blades and more prominent radial grooves (Fig. 38a, e–g); *S. monteithi* is larger with squiggly apical cords and a more protruded spire (Fig. 41c, e). Anatomically the incomplete secondary ureter and coiled, reflexed primary ureter immediately distinguish *S. seticostata* from other sympatric charopids reviewed in this study.

PREVIOUS STUDIES

Hedley (1924) tentatively assigned this species to the New Zealand *Suteria* Pilsbry, 1892 on the basis of overall similarity to *Suteria ide* (Gray, 1850) which also has periostracal setae. However, different apical sculpture of *S. ide* indicates that setal processes in the two species are convergent.

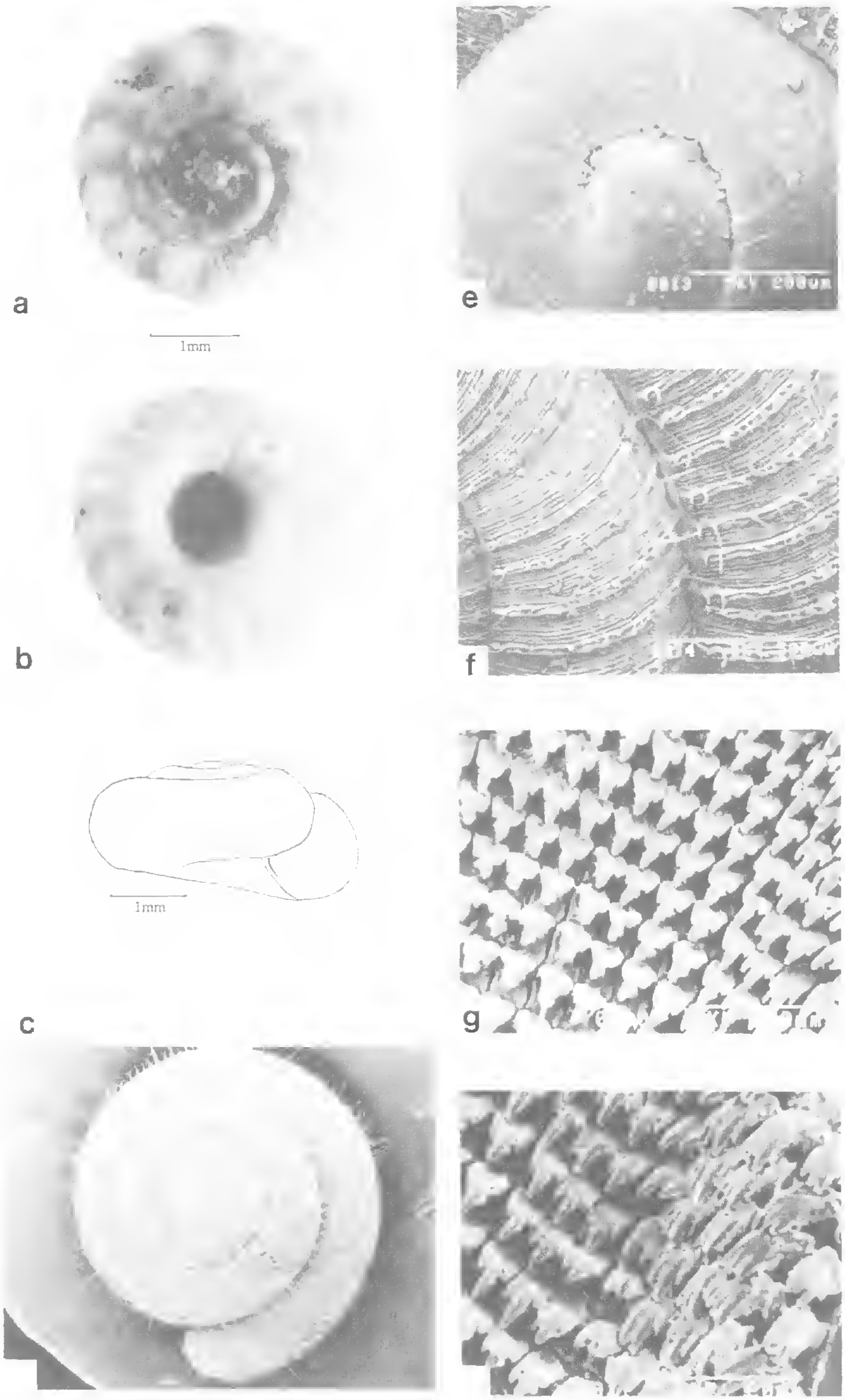
TYPE MATERIAL

HOLOTYPE: AMC63511, Dorrigo, NSW, under logs. Collected by S.W. Jackson, Nov. 1910. Height of shell 1.87 mm, diameter 3.58 mm, H/D ratio 0.52, D/U ratio 2.90, whorls 4 5/8+.

PARATYPES: AMC63685, 3 specimens, same locality data as holotype.

OTHER MATERIAL

NEW SOUTH WALES: Clarence River (5, AMC142467, Cox coll.): Tooloom Scrub, Beaury S.F. (28°29'S. 152°24'E), NVF (7, QMMO10937, AMC128533, 15 Mar 1981, AM/QM - ABRS); Woodenbong Ck, S slope of Mt Clunie (28°20'S, 152°30'E), rainforest (15, QMMO10979, AMC128585, 15 Mar 1981, AM/QM - ABRS); W slope Wilsons Peak, top of Condamine River valley (28°16'S, 152°28'E) (2, AMC128635, 16 Mar 1981, AM/QM - ABRS): N of Dorrigo, c. 1.5 km along


a
1mm
b
1mm
c
e
f
g

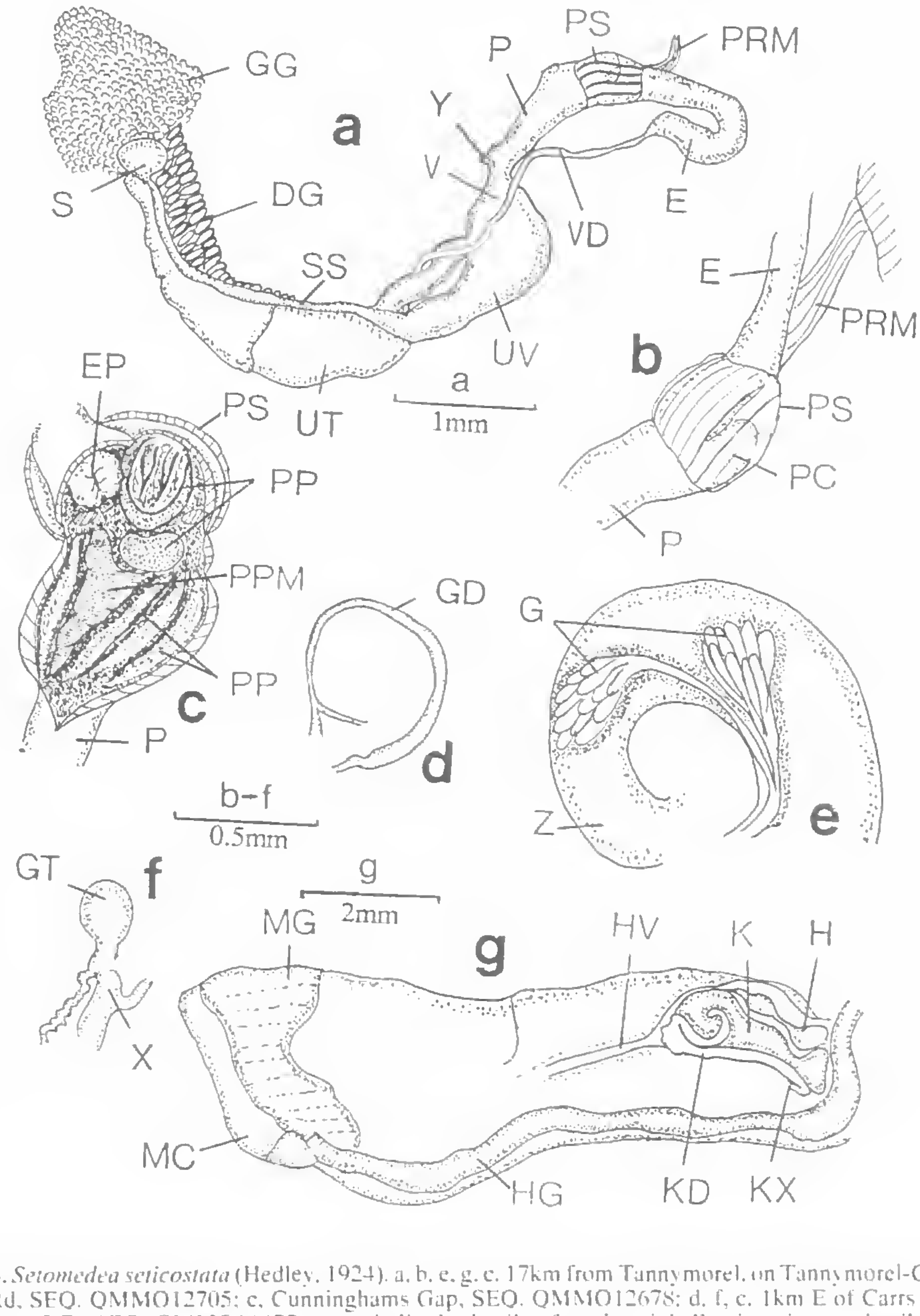


FIG. 33. *Setomedea seticostata* (Hedley, 1924). a, b, e, g, c. 17km from Tannymorel, on Tannymorel-Cambubal S.F. Rd, SEQ. QMMO12705; c, Cunninghams Gap, SEQ. QMMO12678; d, f, c. 1km E of Carrs Lookout, Koreelah S.F., SEQ. QMMO16477. a, genitalia; b, details of penis/epiphallus junction; c, details of penis interior; d, hermaphroditic duct; e, ovotestis; f, talon; g, pallial cavity.

FIG. 32. *Setomedea seticostata* (Hedley, 1924). a–c, Dorrigo, NSW. AMC63511, holotype; d, Acacia Plateau, Koreelah S.F., NSW, QMMO10952; e–f, Mt Glorious, SEQ. QMMO14164; c. 1km E of Carr's Lookout, Koreelah S.F., SEQ. QMMO16477. a–c, entire shell; d, whole shell showing setae; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale lines as marked.

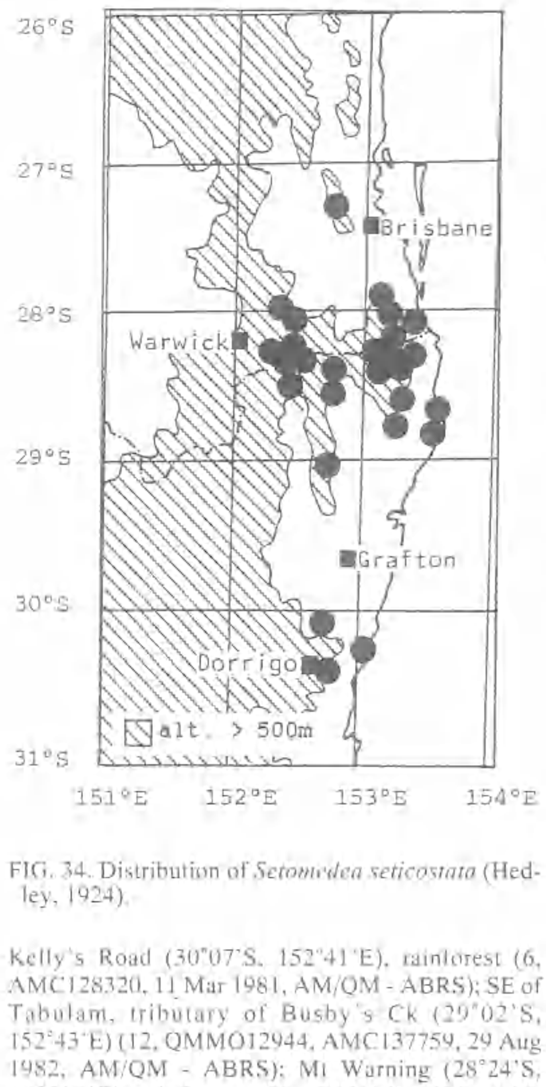


FIG. 34. Distribution of *Setomedea seticostata* (Hedley, 1924).

Kelly's Road (30°07'S, 152°41'E), rainforest (6, AMC128320, 11 Mar 1981, AM/QM - ABRS); SE of Tabulam, tributary of Busby's Ck (29°02'S, 152°43'E) (12, QMMO12944, AMC137759, 29 Aug 1982, AM/QM - ABRS); Mt Warning (28°24'S, 153°17'E) rainforest (22, QMMO10499, AMC129302, 19 Mar 1981, AM/QM - ABRS); Toonumbar S.F., c. 34 km from Kyogle on Toonumbar forest road (28°33'S, 152°45'E) (3, QMMO10908, AMC128498, 14 Mar 1981, AM/QM - ABRS); Wiangarie S.F., c. 25 km NE of Kyogle (28°23'S, 153°06'E), 1000 m (7, AMC142481, 17 May 1976, P.H. Colman, I. Loch); Red Scrub F.R., Whian Whian S.F. (28°38'S, 153°19'E), 210 m (1, AMC142484, 15 May 1976, P.H. Colman, I. Loch); Dorrigo (23, AMC63760, S.W. Jackson); Koreelah S.F., Acacia Plateau, (28°21'S, 152°24'E), SEVT/MVF (47, AMC128554, QMMO10952, 15 Mar 1981, AM/QM - ABRS); Beaury S.F., c. 15 km W of Urbenville (28°21'S, 152°24'E), 810 m (2, AMC142483, 18 May 1976, P.H. Colman, I. Loch); Rocky Ck, Red Scrub F.R., (28°38'S, 153°20'E), rainforest (9, QMMO10404, AMC128865, 20 Mar 1981, AM/QM - ABRS); Terania Ck (28°34'S, 153°19'E), 340 m (1, AMC142482, 16 May 1975, P.H. Colman, I. Loch); Ballina (2, AMC11108, ex C. Hedley); Tweed River (4, AMC142485, ex Cox, ex Petterd); Murwillumbah, under logs (1, AMC28488, 3 Dec 1907, C.F. Laseron); Lismore (2, AMC5784, ex C. Hedley); Dorrigo (5, AMC63772, S.W. Jackson); Bryon Bay (3, AMC4312, ex Cox); Big Scrub, Murwillumbah (3, AMC103795, Lower, ex Cox); Richmond River, Lismore, in scrub under decayed timber (1, AMC63872, ex Brazier); Sherrard Falls, Dorrigo, warm temperate rainforest, litter, 600 m (1, QMMO16776, 3 Nov 1983, AM/QM - ABRS); c. 1.5 km E along Kelly's Rd in dense rainforest, Cloud's Creek S.F., (30°07'S, 152°41'E) (3, QMMO10773, AMC128320, Mar 1981, AM/QM - ABRS); along Croftby Rd, top of Condamine River Valley, (28°15'S, 152°29'E) (1, QMMO10540, Mar 1981, AM/QM - ABRS); c. 5.5 km E of Dorrigo, (30°23'S, 152°44'E) (4, QMMO10796, AMC128351, Mar 1981, AM/QM - ABRS 1981); Tooloom Scrub, Beaury S.F., under logs, NVF (3, QMMO16900, 4 May 1986, J. Stanisic, J. Chaseling); Mt Glennie 16 km E of Woodenbong, 900 m (3, QMMO11933, 24 Oct 1982, G.B. Monteith, D. Yeates); c. 1.5 km from summit of Mt. Warning, (28°24'S, 153°16'E) (3, QMMO10515, AMC129319, Mar 1981, AM/QM - ABRS); Mt Warning, CNVF (28°24'S, 153°16'E) (2, QMMO12737, AMC136831, 15 Dec 1981, AM/QM - ABRS); Swan's Rd, Bruxner Park Flora Reserve, subtropical rainforest, under logs (6, QMMO14768, 14 Nov 1983, AM/QM - ABRS).

SOUTH-EAST QUEENSLAND: Lower Ballanjui Falls track, Binna Burra, Lamington N.P., under logs (3, QMMO16551, 25 Sept 1986, J. Stanisic); Burleigh Heads N.P., under logs, vine thicket (2, QMMO16922, 21 Jan 1987, J. Stanisic, D. Potter); c. 3 km SE of summit Mt Glorious, NVF (27°20'S, 152°46'E) (3, QMMO11990, QMMO11994, AMC136419, 2 Dec 1982, AM/QM - ABRS); c. 25.2 km from Goomburra, Goomburra S.F., NVF/Palms/*Araucaria* (27°59'S, 152°21'E) (5, QMMO11121, AMC128618, 16 Mar 1981; 7, QMMO12691, 7 Dec 1981, AM/QM - ABRS); Curtis Falls Circuit, Mt Tamborine, litter, CNVF (1, QMMO16436, 23 Feb 1986, J. Stanisic, J. Chaseling); Mt Hobwee Circuit, Binna Burra, Lamington N.P., litter NVF (10, QMMO18868, 1 Oct 1985, J. Stanisic, J. Chaseling, D. Potter); Tullawallal Circuit, Binna Burra, Lamington N.P., under logs, NVF (9, QMMO16737, 2 Oct 1985, J. Stanisic, D. Potter, J. Chaseling); Border Track, Binna Burra, Lamington N.P., under logs, NVF (5, QMMO16871, 10 Mar 1984, J. Stanisic); Maiala N.P., Mt Glorious, NVF (6, QMMO11603, QMMO11848, 20 Jun 1982,

TABLE 9 - LOCAL VARIATION IN *SETOMEDEA SETICOSTATA* (HEDLEY, 1924)
(MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Setomedea seticostata												
Dorrigo AMC 63511 (Holotype)	1	4 5/8+	1.87	3.58	0.52	0.26	1.15	0.22	61	5.42	1.23	2.91
QMMO 10796	1	5 1/8	2.34	4.47	0.52	0.26	1.24	0.21	—	—	1.54	2.90
Binna Burra QMMO 16551	2	5 (4 7/8–5 1/8-)	2.03±0.235 (1.79–2.26)	4.00±0.170 (3.83–4.17)	0.51±0.035 (0.47–0.54)	0.24±0.065 (0.17–0.30)	1.24	0.19±0.050 (0.14–0.24)	67	5.56	1.36±0.045 (1.31–1.40)	2.96±0.035 (2.92–2.99)
QMMO 16578	1	5 1/8-	2.17	3.83	0.57	0.30	1.28	0.23	—	—	1.27	3.01
O'Reillys QMMO 10427	1	4 7/8	1.75	3.75	0.47	0.17	1.19	0.14	71	6.02	1.34	2.81
Tooloom Scrub QMMO 16900	1	5 1/4	2.17	4.17	0.52	0.30	1.32	0.23	94	7.16	1.34	3.13
Koreelah S.F. QMMO 16477	2	5+ (5 - to5 1/8)	2.18±0.085 (2.09–2.26)	4.05±0.215 (3.83–4.26)	0.54±0.050 (0.49–0.59)	0.26±0.045 (0.21–0.30)	1.26±0.020 (1.24–1.38)	0.21±0.035 (0.17–0.24)	-	—	1.38±0.105 (1.27–1.48)	3.00±0.115 (2.88–3.11)
Hall's Plain QMMO 16895	1	5 1/8	2.17	4.05	0.54	0.30	1.28	0.23	-	—	1.36	2.99
Mt Glennie QMMO 11933	2	4 7/8 (4 7/8-to4 7/8)	1.96±0.40 (1.92–2.00)	3.75±0.130 (3.62–3.88)	0.53±0.005 (0.52–0.53)	0.23±0.064 (0.17–0.30)	1.22±0.025 (1.19–1.24)	0.19±0.050 (0.14–0.24)	71.5±3.50 (68–75)	6.09±0.505 (5.58–6.59)	1.23±0.040 (1.19–1.27)	3.04
Mt Glorious QMMO 14164	1	4 5/8	1.83	3.41	0.54	0.21	1.15	0.19	72	6.72	1.15	2.96

MSA party); Koreelah S.F., Acacia Plateau, under logs, NVF/MVF (1, QMMO16796, 4 May 1986, J. Stanisic, J. Chaseling); Lower Ballanjui Falls Circuit, Binna Burra, Lamington N.P., NVF, litter (7, QMMO16892, 30 Sept 1985, J. Stanisic, D. Potter, J. Chaseling); O'Reillys, Lamington N.P., (28°14'S, 153°15'E) MVF (13, QMMO10427, 17 Mar 1981, AM/QM - ABRS); Mt Glorious, NVF, litter (3, QMMO14164, 28 Nov 1983, J. Stanisic); Araucaria Track, Binna Burra, Lamington N.P., under logs, NVF (7, QMMO16578, 27 Sept 1986, J. Stanisic); c. 1 km E of Carrs Lookout, Koreelah S.F., under logs, NVF (10, QMMO16477, 3 May 1986, J. Stanisic, J. Chaseling); Border Track, Binna Burra, Lamington N.P., under logs, NVF, (9, QMMO16877, J. Stanisic, 31 Mar 1984); Hall's Plain, E of Emu Vale, under logs, CNVF, (4, QMMO16895, 4 May 1986, J. Stanisic, J. Chaseling) Cunninghams Gap, (1, QMMO6070, 21 Mar 1977, M.J. Bishop); Binna Burra, Lamington N.P., CNVF, 850 m (28°13'S, 153°12'E) (1, QMMO6073, Apr 1976, M.J. Bishop); The Knoll N.P., Mt Tamborine, palm gully (27°55'S, 153°10'E) (1, QMMO6305, 3 Aug 1976, M.J. Bishop); initial part of Kweebani Caves Walk, Binna Burra, Lamington N.P. under logs, NVF (3, QMMO16884, 9 Mar 1984, J. Stanisic); Cunninghams Gap, near monument, 755 m, NVF (28°04'S, 152°24'E) (8, QMMO12678, AMC136807, 7 Dec 1981, J. Stanisic; 2, AMC128605, 16 Mar 1981, J. Stanisic, D. Potter; 3, QMMO16901, 5 May 1986, J. Stanisic, J. Chaseling); Upper Pine Creek, via Canungra, under bark of fallen tree, rainforest with *Araucaria* (6, QMMO16904, J. Stanisic, D. Potter, 21 Jan 1987); Coomera Falls Track, Binna Burra Lamington N.P., NVF, under log (1, QMMO16575, 26 Sept 1986, J. Stanisic); Nagarigoon Falls Track, Binna Burra, Lamington N.P., under logs, NVF (1, QMMO16883, 20 Apr 1986, J. Stanisic, J. Chaseling); c. 17 km from Tannymorel, on Tannymorel-Cambubal S.F. Rd, 1000 m, MVF/Araucaria (3, QMMO12705, AMC136819, 7 Dec 1981, AM/QM - ABRS 1981); Mt Glorious, in litter and under logs, NVF (3, QMMO16128, 26 Jan 1986, J. Stanisic, J. Chaseling); Natural Bridge N.P., (28°13'S, 153°14'E), NVF (7, QMMO10452, QMMO10461, AMC129265, 18 Mar 1981, AM/QM - ABRS).

Diagnosis

Shell strongly depressed, diameter 3.41–4.47 mm (mean 3.91 mm), with 4 5/8 to 5 1/4 (mean 5-) normally coiled whorls. Last whorl descending slightly more rapidly. Spire elevated, apex slightly sunken to elevated, SP/BWW ratio 0.14–0.24 (mean 0.20), height 1.75–2.34 mm (mean 2.05 mm). H/D ratio 0.47–0.59 (mean 0.52). Protoconch glossy, of 1 1/2 to 1 5/8 whorls, mean diameter 628.6μm at 1 1/2 whorls. Apical sculpture of continuous low, narrow spiral cords and a few curved radial growth ridges (Fig. 32e). Post nuclear sculpture of prominent radial ribs, regularly spaced, 61-94 (mean 72.6) on body whorl (Fig. 32f). Ribs/mm 1.15-1.54 (mean 1.32). Major ribs slightly scalloped. formed by two raised radial ribs the first of which has periostracal setae at regular intervals along its length (Fig. 32f). Microsculpture of fine radial riblets, 6-12 between each set of major ribs, whose interstices are 6-8 times their width, and fine, crowded spiral cords which are also visible on the apical surface of the radials (Fig. 32f). Shell surface with weak spiral furrows. Sculpture continuous on the base (Fig. 32b). Umbilicus large, diameter 1.15–1.54 mm (mean 1.32 mm), D/U ratio 2.81–3.13 (mean 2.98), U-shaped. Sutures impressed. Whorls shouldered above and rounded below a slightly compressed periphery. Aperture roundly lunate. Lip simple, columella slightly thickened. Parietal callus developed. Colour yellow-horn with zigzag reddish-brown flammulations which are continued onto the base. Based on 13 measured adults.

Genitalia with epiphallus (Fig. 33a, b) short, muscular, reflexed before entering the penis subapically through a simple pore (Fig. 33c). Penis (Fig. 33c) pear-shaped with apex sheathed to terminal part of epiphallus. Penial caecum present. Apical bulb of penis containing a fleshy, horseshoe-shaped pilaster. Lower penial chamber separated by a muscular collar and containing low fleshy pilasters (Fig. 33c). Penial retractor muscle inserting on the epiphallus.

Central and lateral teeth (Fig. 32g,h) with long, lanceolate mesocone. No data on marginal teeth.

Based on 8 dissected specimens (QMMO16477, QMMO12705, QMMO12678, QMMO16128, QMMO12691).

RANGE AND HABITAT

S. seticostata inhabits warm temperate forests and cool subtropical vine forests of the Great Dividing Range (from Dorrigo, NSW to the Mistake Mountains, SEQ), and the highlands of the McPherson Ranges. The species also occurs in the coastal, moist warm subtropical vine forests, from the Bellinger River, NSW, to the Queensland border, and the unusual coastal vine thickets at Burleigh Heads, SEQ. The northern limit of distribution is the warm subtropical notophyll vine forest of Mt Glorious in the southern D'Aguilar Range, SEQ. Like *Ngairea dorrigoensis*, *S. seticostata* has been collected in drier subtropical forests (vine thickets and microphyll vine forest) in the northern part of the Richmond Range, NSW. It lives under and in moist rotting logs and forest debris.

REMARKS

Early collections of *S. seticostata* include many localities in and around the Big Scrub region of northern NSW. Today *S. seticostata* survives in remnant pockets of this once large rainforest such as the Red Scrub Flora Reserve, NSW (28°38'S, 153°19'E). The microhabitat is the damp, decayed recesses of rainforest floor debris which are generally ignored by other charopid species. Periostracal setae may be an adaptation for surviving in these sticky, damp areas by minimising particle adherance. There is geographic variation in shell parameters but it is not possible to infer trends from the limited adult material available. Although 355 specimens were available for study only 13 were adult and suitable for statistical analysis.

Setomedea nudicostata sp. nov.
(Figs 35–37; Tables 8, 10)

ETYMOLOGY

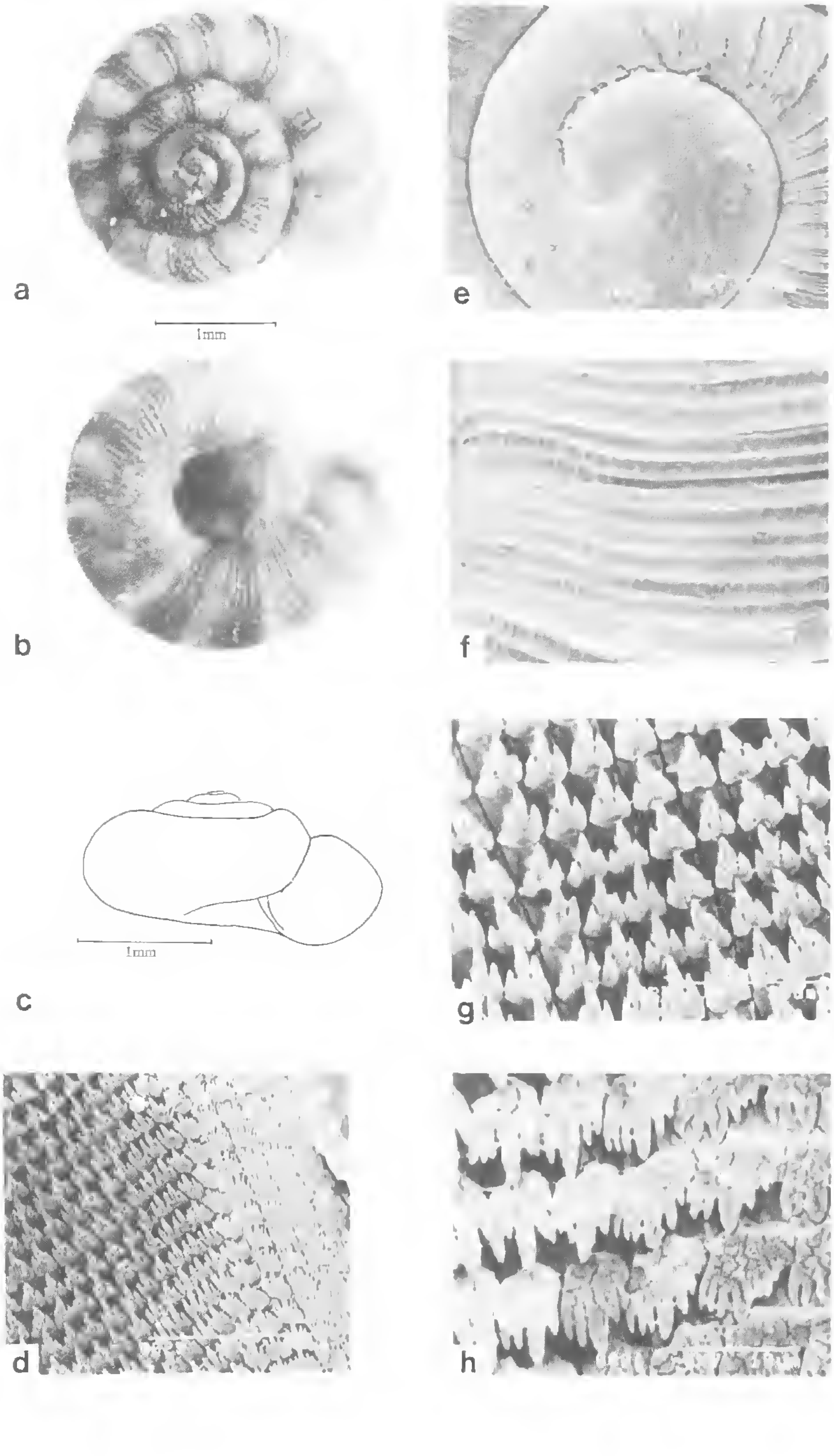
Latin *nudus*, naked; and *costata*, having ribs; referring to the absence of periostracal setae on the major ribs.

COMPARISONS

S. nudicostata lacks periostracal setae. It is further distinguished in the genus by low whorl count (3 7/8+), small size (diameter = 2.86 mm), narrow V-shaped umbilicus (diameter =0.86 mm), flammulated shell, apical sculpture of low, squiggly spiral cords. and numerous curved complex radial ribs on the adult whorls. The sympatric *Gyrocochlea curtisiana* has a flammulated shell and adult sculpture of prominent curved radials (Fig. 54a) but differs in being larger (diameter = 5.78 mm), having an average 4 5/8+ whorls which are strongly shouldered, a convex pitted spire, and very wide umbilicus (diameter = 1.86 mm). *Sinployea intensa* (Fig. 137a, b), is smaller, has fewer but more regular apical spiral cords, more numerous, simple radial ribs on the adult whorls, and a monochrome brown shell. *Omphaloropa varicosa* (Fig. 134e,f) has regular spirals on the protoconch but is much smaller with relatively

TABLE 10 - LOCAL VARIATION IN *SETOMEDEA NUDICOSTATA* SP. NOV., *SETOMEDEA JANAE* SP. NOV. AND *SETOMEDEA MONTEITHI* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS (mm)	HEIGHT (mm)	DIAMETER	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Setomedea nudicostata												
Bobby Range												
QMMO 15168 (Holotype)	1	3 5/8-	1.36	2.68	0.51	0.17	0.81	0.21	70	8.30	0.76	3.53
AMC 142934	1	4	1.70	3.07	0.56	0.30	0.98	0.30	89	9.23	0.88	3.47
QMMO 16593	1	3 3/4	1.45	2.56	0.57	0.26	0.81	0.32	75	9.33	0.72	3.55
Gracemere												
AMC 140498	1	4 1/4-	1.70	3.11	0.55	0.21	0.94	0.23	86	8.80	0.97	3.22
Setomedea janae												
Mt Dryander												
AMC 142469 (Holotype)	1	4 5/8	1.83	3.71	0.49	0.17	1.19	0.14	56	4.81	1.31	2.82
AMC 150092	1	4 1/2-	1.83	3.66	0.50	0.04	1.15	0.04	62	5.38	1.23	2.97
AMC 142468	3	4 3/4- (4 5/8–4 3/4)	1.93±0.136 (1.66–2.09)	3.55±0.074 (3.66–4.31)	0.54±0.027 (0.49–0.58)	0.18±0.027 (0.13–0.21)	1.24±0.042 (1.15–1.28)	0.15±0.023 (0.10–0.17)	53±4.0 (49–56)	4.82±0.025 (4.57–5.07)	1.19±0.046 (1.11–1.27)	3.00±0.164 (2.68–3.23)
Eungella												
AMC 142488	1	4 1/2+	1.83	3.71	0.49	0.13	1.24-	0.10	54	4.63	1.01	3.68
AMC 142470	1	4 1/2-	1.83	3.71	0.49	0.13	1.24	0.10	80	6.87	1.13	3.28
Setomedea monteithi												
Ayton												
AMC 142489 (Holotype)	1	5+	2.94	4.60	0.64	0.51	1.58	0.32	63	4.36	1.44	3.20
AMC 150090	1	4 3/4+	2.47	4.47	0.55	0.26	1.41	0.18	61	4.34	1.29	3.46
AMC 142472	4	5 3/8+ (5 1/4–5 1/2)	3.28±0.047 (3.15–3.37)	5.48±0.111 (5.29–5.71)	0.60±0.16 (0.56–0.63)	0.50±0.030 (0.42–0.55)	1.76±0.021 (1.70–1.79)	0.29±0.018 (0.25–0.32)	74	4.12	1.69±0.053 (1.64–1.85)	3.24±0.070 (3.09±3.43)
Shipton's Flat												
QMMO 15477	1	5 3/8	3.11	3.75	0.83	0.55	1.83	0.30	---	---	1.03	3.65
Mt Finnigan												
QMMO 15482	4	5 1/8- (4 7/8–5 3/8)	2.42±0.071 (2.26–2.56)	3.68±0.037 (3.62–3.79)	0.66±0.016 (0.62–0.69)	0.44±0.036 (0.34–0.51)	1.36±0.040 (1.24–1.41)	0.32±0.018 (0.28–0.36)	---	---	0.98±0.028 (0.92–1.03)	3.77±0.082 (3.57–3.88)
Mt Lewis												
QMMO 14761	2	5 1/2 (5 3/8– 5 5/8+)	2.64±0.040 (2.60–2.68)	5.11±0.040 (5.07–5.15)	0.52±0.015 (0.50–0.53)	0.26–0.045 (0.21–0.30)	1.66	0.16±0.025 (0.13–0.18)	62.0±1.00 (61–63)	6.26±1.00 (5.80–6.71)	1.66±0.020 (1.64–1.68)	3.07±0.010 (3.06–3.08)
Mt Bellenden Ker												
QMMO 15805	1	5 1/8	2.13	4.00	0.53	0.26	1.36	0.19	64	5.08	1.27	3.14
QMMO 11346	1	5+	2.04	3.75	0.55	0.09	1.62	0.05	50	4.24	1.23	3.04


a
1mm
b
c
1mm
d
e
f
g
h

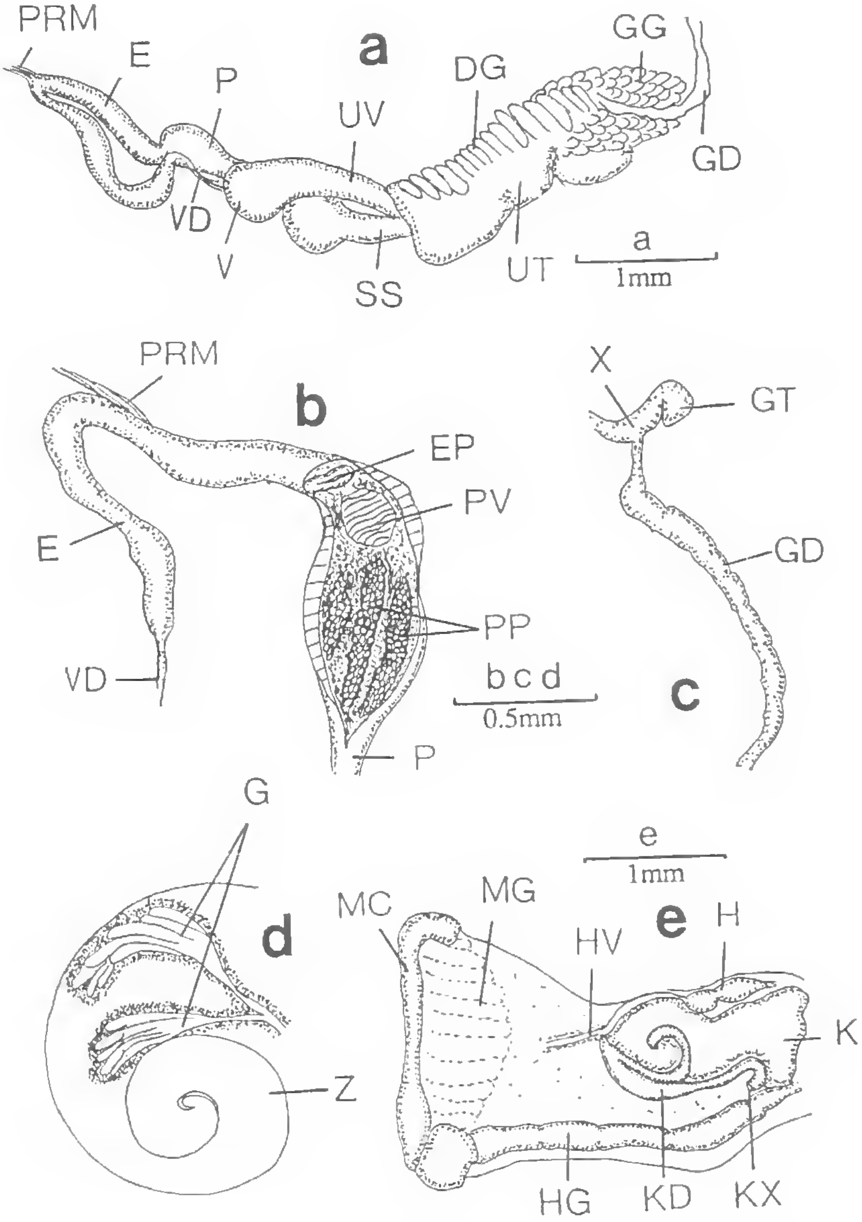


FIG. 36. *Setomedea nudicostata* sp. nov. a, c–e, Granite Creek, on Bobby Range Rd. 5.2 ml E of Bulburin Forestry Station, SEQ. AMC142934, paratype; b, Mt. Booroon Booroon, Bobby Range, SEQ. QMMO16593, paratype. a, genitalia; b, details of penis interior and penial retractor muscle insertion; c, talon and hermaphroditic duct; d, ovotestis; e, pallial cavity. Scale lines as marked.

FIG. 35. *Setomedea nudicostata* sp.nov. a–c, Foothills of Bobby Range, Granite Ck, SEQ, QMMO15168, holotype; d, g–h, Granite Ck on Bobby Range Rd, SEQ. AMC142934, paratype; e–f, Mt Booroon Booroon, Bobby Range, SEQ. QMMO16593, paratype. a-c, entire shell; d, marginal teeth; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, details of marginal teeth. Scale lines as marked.

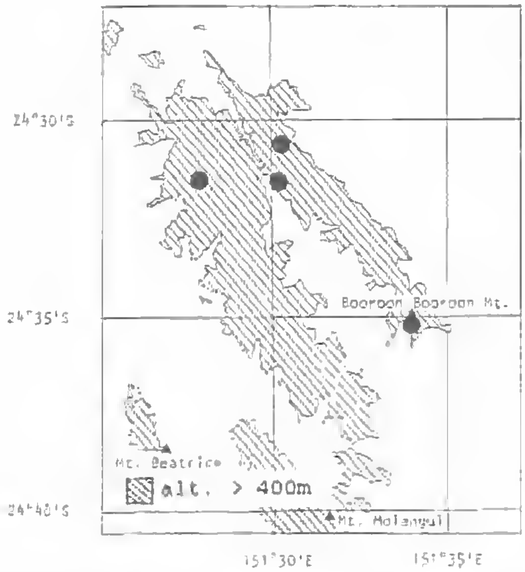


FIG. 37. Distribution of *Setomedea nudicostata* sp. nov. in the Bobby Range area, SEQ.

large umbilicus, and adult sculpture of few very prominent radial ribs with interstices which are strongly reticulate.

Type Material

Holotype: QMMO15168, foothills of Bobby Range, Granite Creek, SEQ (24°30.7'S, 151°30.3'E), under leaf litter. Collected by Terry Carless, 4 December 1983. Height of shell 1.36 mm, diameter 2.68 mm, H/D ratio 0.51, D/U ratio 3.53, whorls 3 5/8.

Paratypes: Granite Creek on Bobby Range Road, 5.2 miles E of Bulburin Forestry Stn, SEQ (2, AMC142934, 8 May 1975, J.B. Burch); Mt Booroon Booroon, Bobby Range, SEQ, base, NVF along creek, under logs (3, QMMO16593, 17 Sept 1986, J. Stanisic, D. Potter); c. 17.9 km E of Builyan, on Builyan-Bulburin S.F. Rd., Bulburin S.F., SEQ, (24°33'S, 151°27'E), under bark, MVF (12, QMMO21862, 29 Jun 1989, J. Stanisic, D. Potter, J. Chaseling).

Other Material

Gracemere, near Rockhampton, MEQ (1, AM-C140498, 1887, C.T. Musson).

Diagnosis

Shell small, diameter 2.56-3.11 mm (mean 2.86 mm) of 3 5/8 to 4 1/4 (mean 3 7/8 +) loosely coiled whorls. Apex and spire moderately elevated, SP/BWW ratio 0.21-0.32 (mean 0.27), height 1.36-1.70 mm (mean 1.55 mm), H/D ratio 0.51-0.57 (mean 0.55). Last whorl descending only slightly or not at all. Protoconch exsert, 1 3/8 to 1 1/2 whorls, mean diameter 719μm at 1 1/2 whorls. Apical sculpture (Fig. 35e) of fine spiral cords with curved radial ridges toward the terminal part of the protoconch. Post nuclear sculpture (Fig. 35f) of prominent widely spaced, protractively sinuated radial ribs, 70-89 ribs (mean 80) on the body whorl. Ribs/mm 8.30-9.33 (mean 8.92). Microsculpture (Fig. 35f) of fine radial riblets, 4-9 between each pair of major ribs, crossed by closely spaced, fine spiral cords. Sculpture continuous on base (Fig. 35b). Umbilicus wide, broad V-shaped, diameter 0.72-0.97 mm (mean 0.83). D/U ratio 3.22-3.55 (mean 3.44). Sutures strongly to deeply impressed. Whorls rounded above and flattened below a rounded periphery. Aperture roundly lunate. Lip simple, columella only slightly dilated. Parietal callus moderately developed. Colour yellow-horn with reddish-brown flammulations in a radial pattern. Based on 4 measured adults.

Ovotestis two clumps of palmately clavate alveoli, embedded in the digestive gland just above the stomach. Epiphallus internally with longitudinal thickenings, entering penis apically through a simple pore (Fig. 36b). Penis (Fig. 36b) short, cylindrical, apically with a transversely sculptured, spatulate verge. Remainder of penis with low pustules arranged longitudinally (Fig. 36b). Penial retractor muscle originating on the diaphragm and inserted on the epiphallus.

Central and lateral teeth of radula (Fig. 35g) tricuspid with long lanceolate mesocone and shorter ectocones.

Based on 2 dissected specimens (AM-C142934, QMMO16593).

Range and Habitat

S. nudicostata is known from a handful of specimens found in warm moist notophyll vine forests of the Bobby Range area, SEQ. The single specimen collected by C.T. Musson from Gracemere near Rockhampton, SEQ, has been included because of its historical significance. However, I consider that the locality is wrong and probably the result of a labelling error. *S. nudicostata* lives under logs and bark.

Remarks

The absence of periostracal setae and altered coiling pattern in *S. nudicostata* are major departures from typical *Setomedea*.

Setomedea janae sp. nov.
(Figs 38–40; Tables 8, 10)

ETYMOLOGY

For Jan Chaseling who accompanied me on numerous collecting trips.

COMPARISONS

The squiggly, apical spiral cords, curved radial ribs, periostracal setae and flammulated shell combine to separate *S. janae* from other sympatric charopids. *'Gyrocochlea' iuloidea* (Forbes, 1851) from Port Molle (= Airlie Beach), MEQ, is larger with monochrome brown shell, depressed spire, simple conspicuous radial ribs, greater whorl height, and has no periostracal setae. *Biomphalopa recava* (Fig. 57a,b,c) from the Eungella region, has a much larger, biconcave, flammulated shell with apical sculpture of vague pits, and no periostracal setae. *S. janae* can be distinguished from its congeners by its small whorl count, almost regular spiral cords (Fig. 38e), and strongly scalloped periostracal blades on major radial ribs (Fig. 38f, g).

TYPE MATERIAL

HOLOTYPE: AMC142469, Mt Dryander, 10 miles E of Proserpine, MEQ. Collected by L. Price, 16 June 1958. Height 1.83 mm, diameter 3.71, D/U ratio 2.82, H/D ratio 0.49, whorls 4 5/8.

PARATYPES: Mt Dryander, 10 miles E of Prosperine, MEQ (1, AMC150092, 16 Jun 1958, L. Price; 3, AMC142468, 4 Jul 1964, L. Price); Eungella Range, 50 miles W of Mackay, MEQ (2, AMC142470, Sept 1957, L. Price); Olmara Hills, near Eungella, W of Mackay, MEQ, rainforest (1, AMC142488, Apr 1975, D.K. McAlpine); Dalrymple Heights, Eungella N.P., MEQ (21°02'S, 148°36'E) 1000 m NVF (5, QMMO6371, Nov 1976, M.J. Bishop).

OTHER MATERIAL

Mt William N.P., N of Mackay MEQ, 1120 m (21°01'S, 148°36'E) (5, AMC142487, 27 Apr 1975, J.B. Burch, W.F. Ponder, P.H. Colman); Dalrymple Heights N.P., NW of Mackay, MEQ, 1000 m (7, AMC142486, J.B. Burch, W.F. Ponder, P.H. Colman, 28 Apr 1975); Mt Macartney, Cathu S.F., MEQ, stick brushings (20°51'S, 148°33'E) rainforest, 750 m (2, QMMO17155, 22 Apr 1979, G.B. Monteith); Mount William, Eungella N.P., MEQ, rainforest, 1100 m, stick brushings (21°02'S, 148°36'E) (1, QMMO17156, 19 Apr 1979, G.B. Monteith).

DIAGNOSIS

Shell depressed, diameter 3.41-3.71 mm (mean 3.63 mm), with 4 1/2 to 4 3/4 (mean 4 5/8-) normally coiled whorls, last whorl descending more rapidly. Spire elevated, apex flat to slightly elevated (Fig. 38b), SP/BWW ratio 0.04–0.17 (mean 0.12), height 1.66–2.08 mm (mean 1.87 mm), H/D ratio 0.49–0.58 (mean 0.51). Protoconch shiny, of 1 3/8 to 1 5/8 whorls, mean diameter 624.2μm at 1 1/2 whorls. Apical sculpture (Fig. 38e) of continuous, low, narrow spiral cords, only slightly squiggly; and irregular curved radial ribs. Post nuclear sculpture (Fig. 38f) of deep spiral furrows and prominent complex radial ribs, regularly spaced, 49-80 (mean 59.7) on body whorl. Ribs/mm 4.57-6.87 (mean 5.22). Microsculpture (Fig. 38g) of crowded, scalloped radial riblets, 7-14 between each pair of major ribs, crossed by crowded microspiral cords, which continue onto the sides of the radials. Major radial ribs with setal processes at regular intervals. Sculpture and setae continuous on the base. Interstices of the major ribs 7–8 times their width. Umbilicus (Fig. 38b) wide, U-shaped, diameter 1.01–1.31 mm (mean 1.18 mm), D/U ratio 2.68–3.68 (mean 3.11). Sutures impressed. Whorls (Fig. 38c) shouldered above and rounded below a slightly compressed periphery. Aperture roundly lunate. Lip simple, columella slightly thickened. Parietal callus developed. Colour brownish yellow-horn with irregular darker brown suffusions, continuous on the base. Based on 7 measured adults.

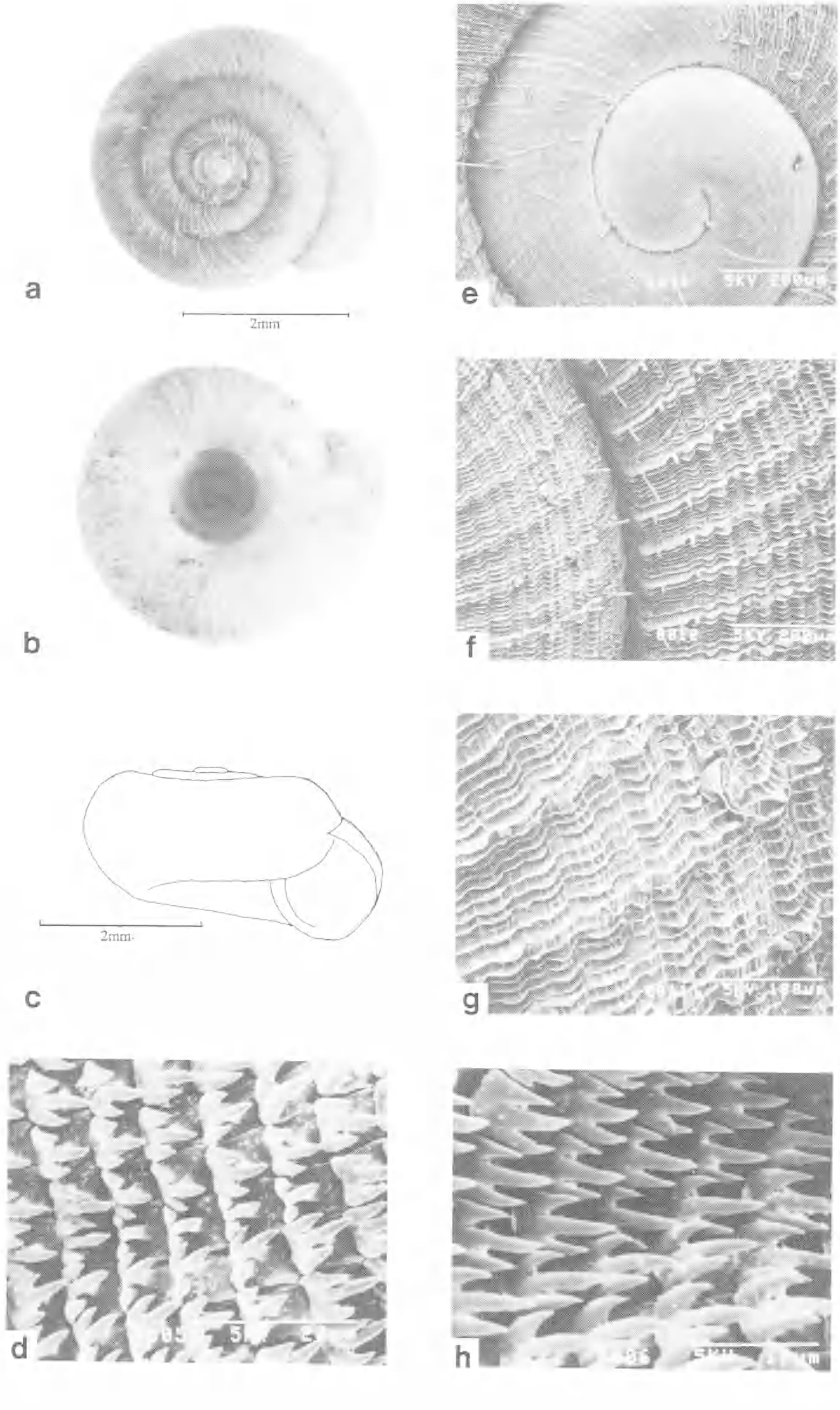
Genitalia with epiphallus (Fig. 39c) shortened and partially incorporated into the penial bulb, opening into the penis apically through a simple pore (Fig. 39c) surrounded by a muscular collar. Lower penial chamber with many raised, corrugated, fleshy, longitudinal pilasters (Fig. 39c). Penial retractor muscle inserted on the epiphallus.

Radula (Fig. 38d, h) without unusual features.

Based on 7 dissected specimens (AMC142486, AMC142487, QMMO6371).

RANGE AND HABITAT

S. janae is restricted to the montane refugia of the Clarke Range in the Eungella area (= Dalrymple Heights), MEQ, with an outlier population on Mt Dryander, north of Proserpine, MEQ. *S. janae* prefers moist warm subtropical notophyll vine forest. Unfortunately no altitude data are available for the records from Mt. Dryander where several forest types are present. The microhabitat of *S. janae* is not known but it has been collected from stick brushings by Dr G.B. Monteith in two separate instances.


a
2mm
b
2mm
c
d
e
f
g
h

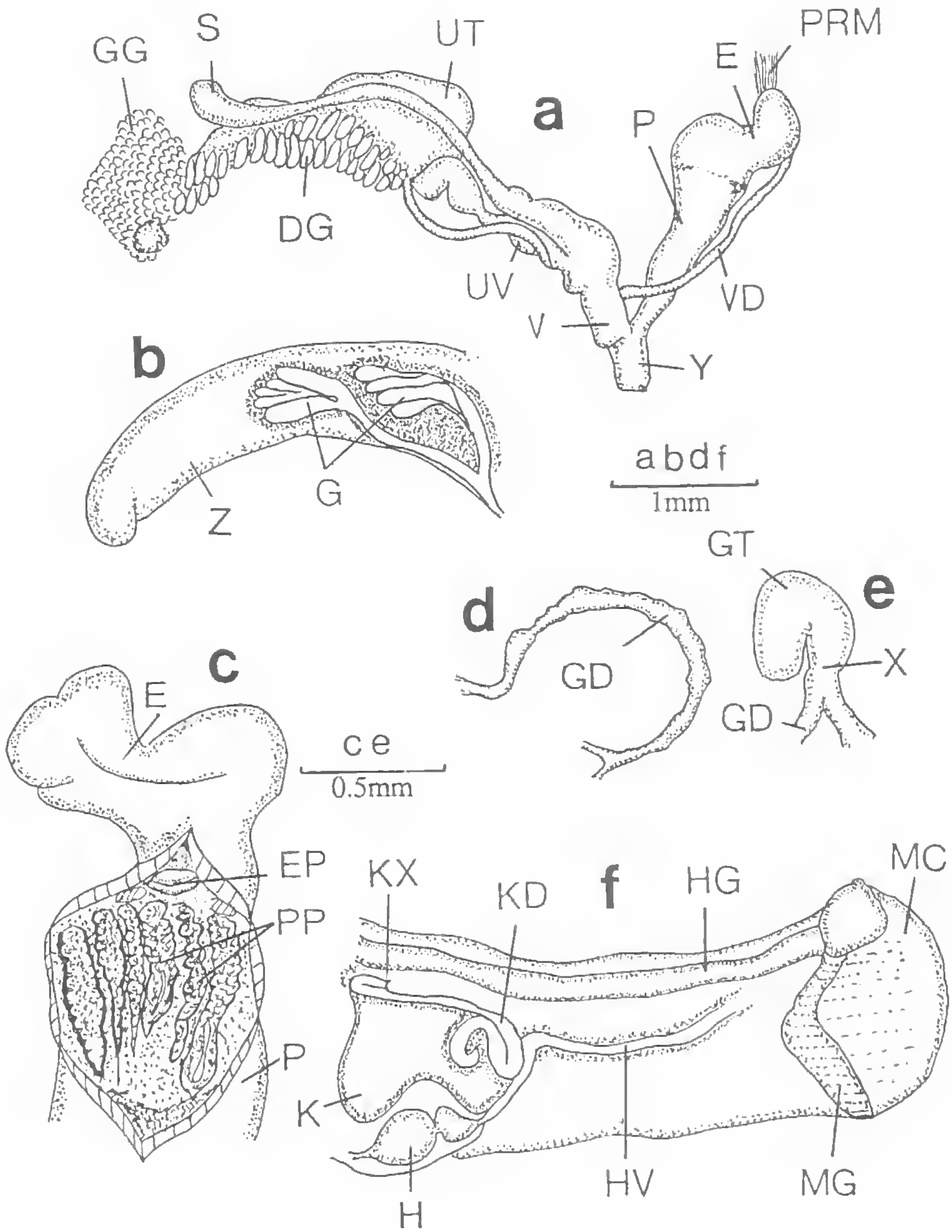


FIG. 39. *Setomedea janae* sp. nov. Dalrymple Heights N.P., NW of Mackay, MEQ. AMC142486. a, genitalia; b, ovotestis; c, details of penis interior; d, hermaphroditic duct; e, talon; f, pallial cavity. Scale lines as marked.

FIG. 38. *Setomedea janae* sp.nov. a–c, Mt Dryander, 10 mls E of Proserpine, MEQ. AMC142469, holotype; e–g, Eungella Range, 50 mls W of Mackay, MEQ. AMC142470, paratype; d, h, Dalrymple Heights, Eungella N.P., MEQ. QMMO6371, paratype. a–c, entire shell; d, central and lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, post nuclear region showing spiral furrows; h, lateral teeth. Scale lines as marked.

REMARKS

S. janae is closely related to *S. seticostata*. The sheathing of part of the epiphallus and apical penial bulb (Fig. 33b) in *S. seticostata* can be readily translated into the compacted epiphallus/penial bulb complex of the fewer-whorled *S. janae* (Fig. 39c). The apical sculptures (Figs 32e, 38e) of the two species are alike and quite different from the squiggly apical cords seen in other *Setomedea*. The exaggerated scalloping of the periostracal blades in *S. janae* (Fig. 38g) can be derived from the *S. seticostata* condition by simple increase in the intensity of the spiral grooving.

Setomedea monteithi sp. nov.
(Figs 41–43; Tables 8, 10)

ETYMOLOGY

For Dr G.B. Monteith in recognition of his efforts in collecting material used for this study.

COMPARISONS

S. monteithi is the largest species of the genus with mean whorl count 5 1/4-, average shell diameter 4.60 mm, and average shell height 2.78 mm. The large size, squiggly apical cords, tight coiling pattern, and weakly scalloped periostracal rib blades, distinguish *S. monteithi* from its congeners. *S. seticostata* (Fig. 32) is smaller with regular apical cords; *S. janae* (Fig. 38) has fewer whorls, strongly scalloped periostracal blades and regular apical cords; and *Setomedea* sp. (Fig. 44) is smaller, with looser coils and narrower umbilicus. *Oreokera cumulus* Odhner, 1917 and *O. nimbus* Stanisic, 1987 have high spired, keeled, flammulated shells with strong radial sculpture and no periostracal setae (Stanisic, 1987, pls 1,2). *Biomphalopa concinna* has a smaller, tesselated, biconcave shell with prominent radials and wide umbilicus (Fig. 60). *'Endodonta' intermedia* Odhner, 1917 has a very small monochrome brown shell with more crowded radial ribs and no setae.

TYPE MATERIAL

HOLOTYPE: AMC142489, Twelve Mile Scrub, near Ayton, Bloomfield River, NEQ, 90 m (15°50'S, 145°19'E). Collected by P.H. Colman, 25 Oct. 1975.

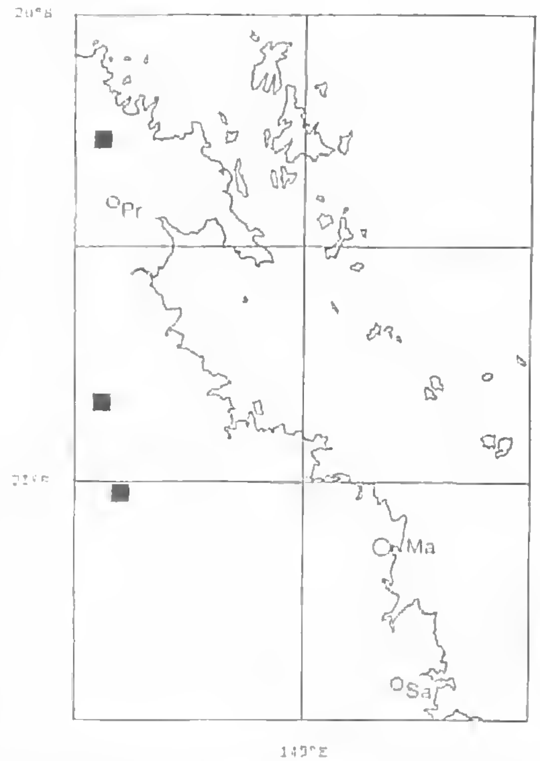
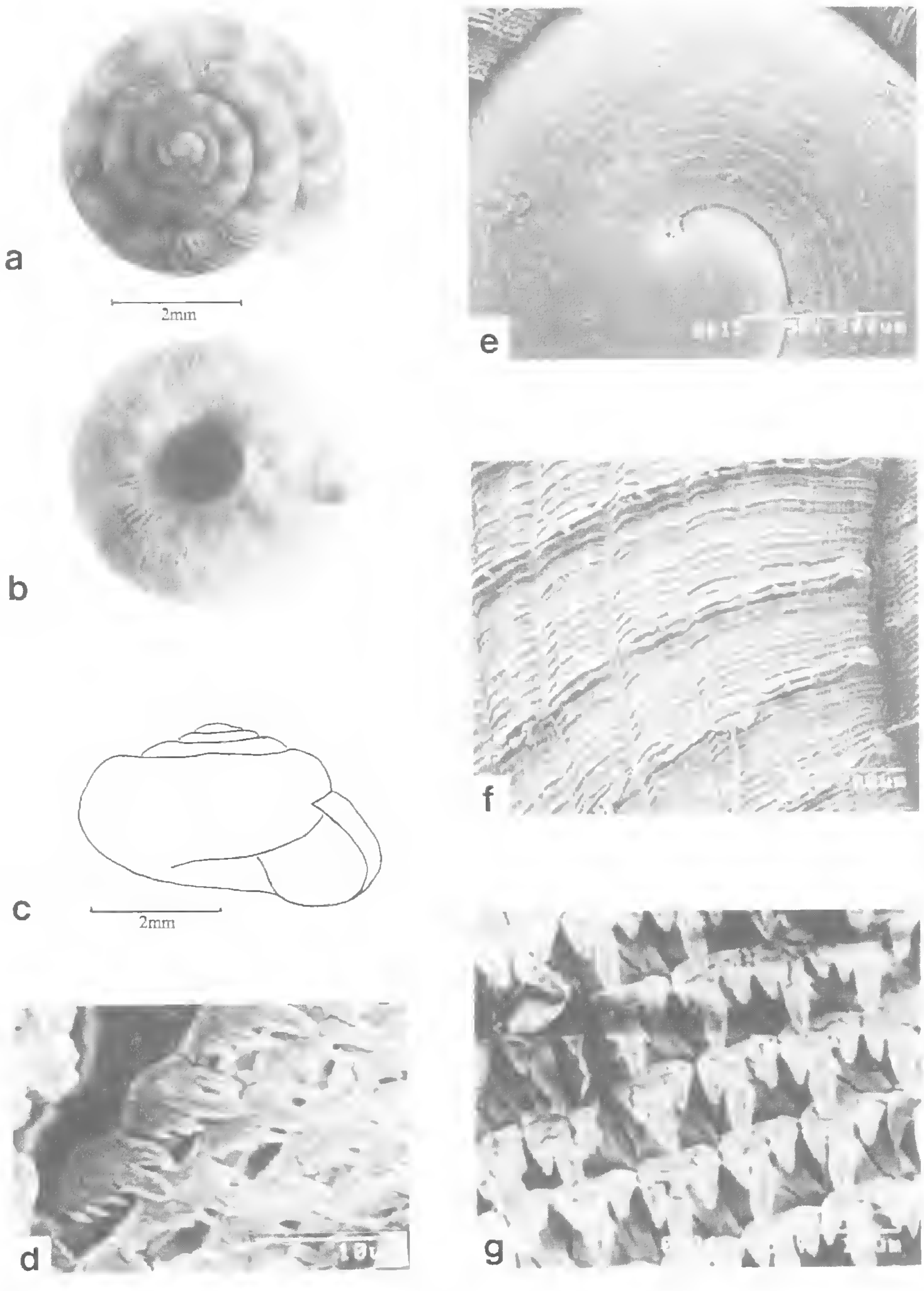


FIG. 40. Distribution of *Setomedea janae* sp.nov. in mid-east Queensland. (Pr = Prosperine; Ma = Mackay; Sa = Sarina).

Height of shell 2.94 mm, diameter 4.60 mm, H/D ratio 0.64, D/U ratio 3.20, whorls 5+.

PARATYPES. NORTH-EAST QUEENSLAND - AMC150090, 5 specimens, same locality data as holotype; Mt Sorrow, Cape Tribulation, 300-800 m, rainforest (5, QMMO17161, 15 Oct 1980, G.B. Monteith); Mt Lewis, c. 17.8 km along Julatten-Mt Lewis Rd, MFF, litter (6, QMMO14761, 27 Jun 1983, J. Stanisic, D. Potter); Gap Creek, Ayton, Bloomfield River, lowland rainforest (4, AMC142472, R. Radnell, 1975); Fritz Creek S.F., near Ayton, Bloomfield River, 30 m (15°50'S, 145°21'E) (28, AMC150089, 24 Oct 1975, P.H. Colman); Mt Finlay S.F., near Ayton, Bloomfield River, 245 m (15°50'S, 145°20'E) (7, AMC150088, 25 Oct 1975, P.H. Colman); Charmillan Creek Crossing, on Ravenshoe - Tully Falls Rd, NVF (17°42'S, 145°31'E) (3, QMMO14754, 28 Sept 1980, J. Stanisic); Mt Bartle Frere, summit centre

FIG 41. *Setomedea monteithi* sp nov. a–c, Twelve Mile Scrub, near Ayton, Bloomfield River, NEQ, AMC 142489, holotype; d, g, Fritz Creek S.F., near Ayton, Bloomfield River, NEQ, AMC 150089, paratype; e–f, same data as holotype, AMC 140090, paratype. a-c, entire shell; d, marginal teeth; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth. Scale lines as marked


a
2mm
b
c
2mm
d
e
f
g

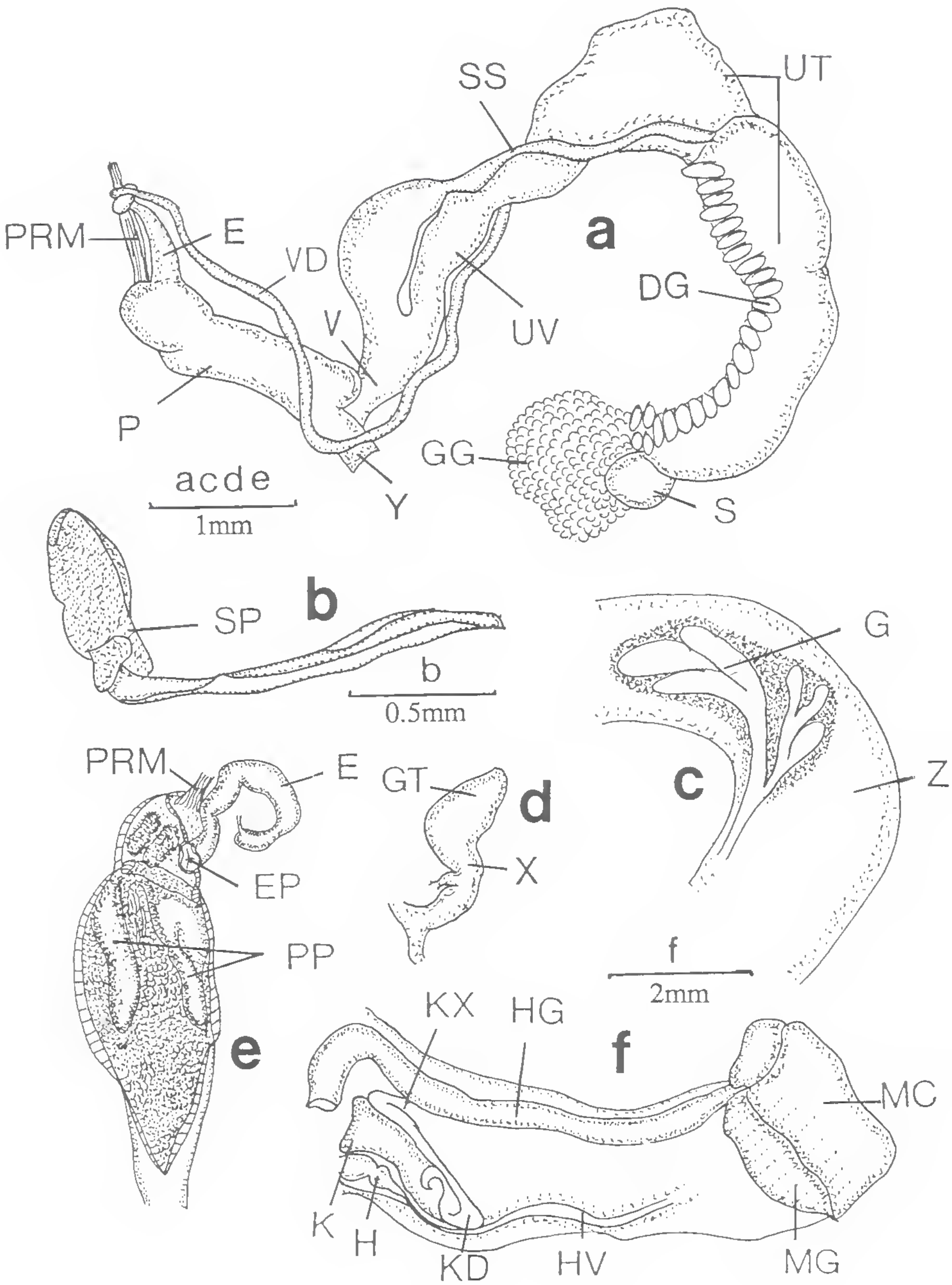


FIG. 42. *Setomedea monteithi* sp.nov. a, b, d, f, Mt Finlay S.F., near Ayton, Bloomfield River, NEQ. AMC150088, paratype; c, Fritz Creek S.F., near Ayton, Bloomfield River, NEQ. AMC150089, paratype; e, Mt Bellenden Ker, NEQ. QMMO11346, paratype. a, genitalia; b, spermatophore; c, ovotestis; d, talon; e, details of penis interior; f, pallial cavity. Scale lines as marked.

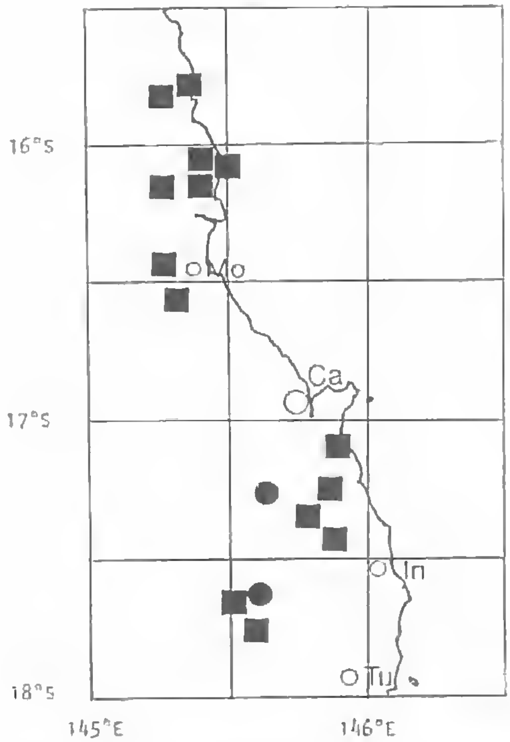


FIG. 43. Distribution of *Setomedea monteithi* sp.nov. (squares), and *Setomedea* sp. (dots) in north-east Queensland. (Mo = Mossman; Ca = Cairns; In = Ingham: Tu = Tully).

peak, 1540 m, SMVFT (17°23'S, 145°48'E) (14, QMMO11411, 7–8 Nov 1981, Earthwatch/QM); Mt Bellenden Ker, 500 m, CMVF (12, QMMO11324, 25–31 Oct 1981, Earthwatch/QM); Mt Bellenden Ker, 1054 m, SNVF (150, QMMO11346, 1–7 Nov 1981, Earthwatch/QM); Mt Finnigan, 37 km S of Cooktown, 850–1100 m, rainforest (7, QMMO15482, 19–22 Apr 1982, G.B. Monteith, D. Yeates, D. Cook); Mt Bartle Frere, NW to centre peak, 1400-1500 m (1, QMMO15495, 24 Sept 1981, G.B. Monteith, D. Cook): Mt Bellenden Ker, summit TV Stn, 1560 m, SMVFT (17°16'S, 145°51'E) (1, QMMO15805, 1–7 Nov 1981 Earthwatch/QM); Shipton's Flat, c. 35 km S of Cooktown, 250 m (1, QMMO15477, 22 Apr 1982, G.B. Monteith, D. Yeates, D. Cook).

OTHER MATERIAL

NORTH-EAST QUEENSLAND: Mt Bellenden Ker, summit, 1560 m, SMVFT (18, QMMO11260, 17-24 Oct 1981, Earthwatch/QM); Leichhardt Creek Crossing, on Mt Lewis Rd, Mt Lewis, under logs, SMVFF (16°36'S, 145°16'E) (1, QMMO14755, 1 Oct 1980, J. Stanisic); 2 km N of Mt Lewis, rainforest, 1000 m, litter (1, QMMO15436, 9 Sept 1981, G.B. Monteith, D. Cook); Noah Creek, via Cape Tribulation, rainforest (1, QMMO17160, 16 Oct 1980, G.B. Monteith); c. 2.5 km N of Mt Lewis, 1040 m (1, QMMO15431, D. Yeates, G. Thompson, 3 Nov 1983); Charmillan creek crossing, on Ravenshoe - Tully Falls Rd, NVF, litter (3, QMMO16231, J. Stanisic, 28 Sept 1980); Mt Bartle Frere, west face, 700–1000 m (1, QMMO17164, G.B. and S.R. Monteith, 7 Oct 1980); North Bell Peak, c. 20 km S of Cairns, 850–1000 m (1, QMMO15493, G.B. Monteith, D. Yeates, G. Thompson, 13 Oct 1982); hill above Daintree River valley, via Daintree CMVF (16°12'S, 145°16'e) (1, QMMO16270, 2 Oct 1980, J. Stanisic); Mt Bartle Frere, walking track below NW peak, c. 1000 m, SNVF (1, QMMO11380, 8 Nov 1981, Earthwatch/QM); Mt Bellenden Ker, summit TV stn, 1560 m, rainforest (17°16'S, 145°51'E) (1, QMMO15800, 1–7 Nov 1981, Earthwatch/QM); Cape Tribulation, lowland rainforest (1, QMMO17162, 12–19 Oct 1980, G.B. Monteith); 2 km N of Cape Tribulation, 50 m, rainforest, stick brushing (16°05'S, 145°28'E) (1, QMMO15525, 2 Oct 1982, G.B. Monteith, D. Yeates, G. Thompson); Mossman Gorge (2, AMC142471, 26 Nov 1963, D.F. McMichael, J.C. Yaldwyn).

DIAGNOSIS

Shell medium to large, diameter 3.62-5.71 mm (mean 4.6 mm) with 4 1/2 to 5 5/8 (mean 5 1/4-) normally coiled whorls, last whorl descending much more rapidly. Spire and apex weakly to strongly elevated, SP/BWW ratio 0.05–0.36 (mean 0.26), height 2.04-3.37 mm (mean 2.78 mm), H/D ratio 0.50–0.83 (mean 0.61). Protoconch glossy, of 1 1/2 to 1 5/8+ whorls, mean diameter 725.1μm at 1 1/2 whorls. Apical sculpture (Fig. 41e) of numerous squiggly spiral cords and a few, weak, curved radial growth ridges. Post nuclear sculpture of complex major radial ribs and broad spiral grooves. Ribs regularly spaced, 50–107 (mean 71.50) on the body whorl. Ribs/mm 4.12–6.71 (mean 4.91). Major ribs consisting of two riblets with high periostracal blades, the one on the apical side with long periostracal setae arranged at regular intervals along its length. Ribs appearing scalloped due to broad spiral undulations in the shell surface. Microsculpture (Fig. 41f) of numerous radial riblets, 7–15 between each pair of major ribs, and fine, closely spaced spiral cords which continue onto the radial ribs. Interstices of major ribs c. 6–8 times their width. Sculpture continued on the base. Umbilicus wide U-shaped, diameter

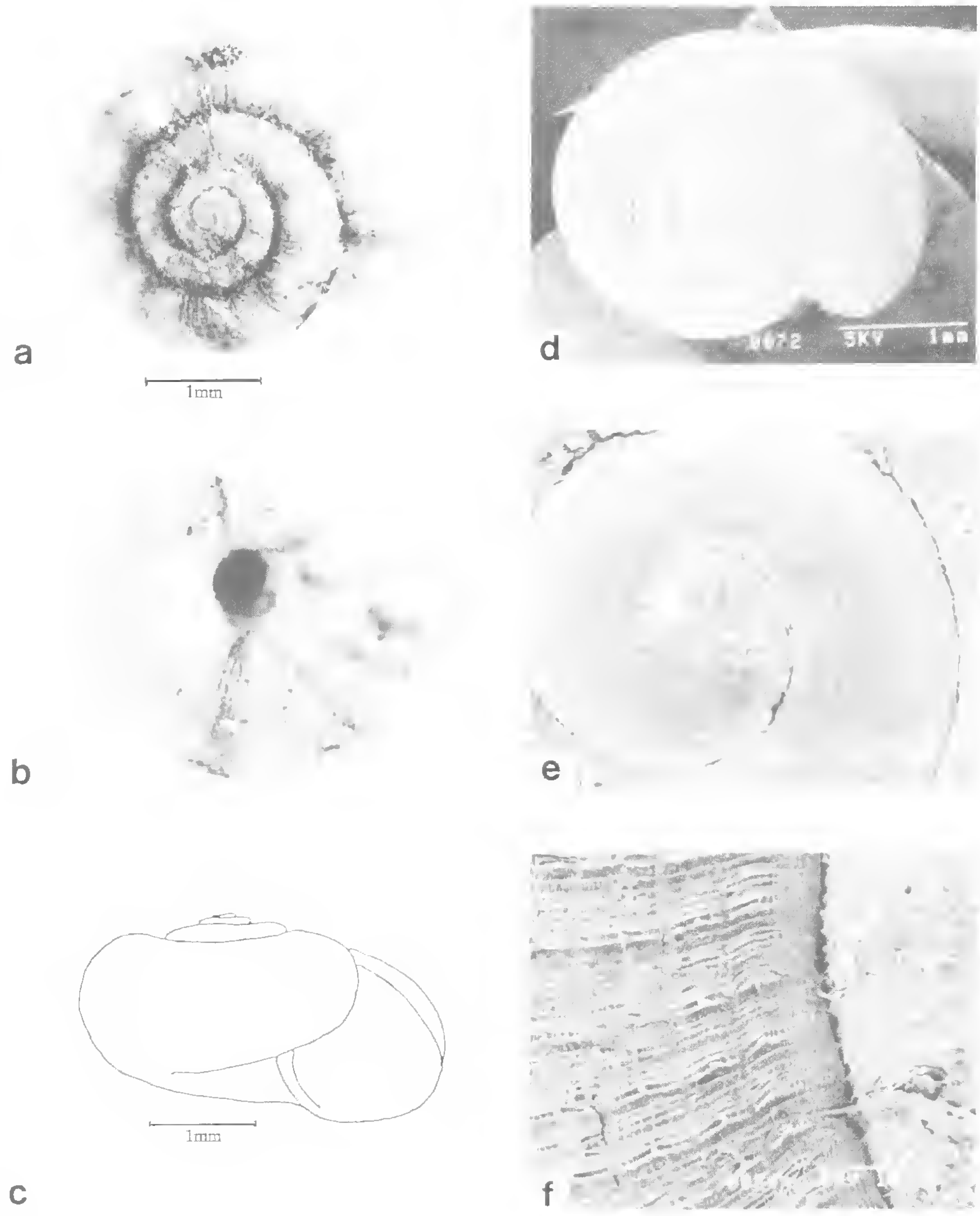


FIG. 44. *Setomedea* sp. a–c, Majors Mtn, 7km SE Ravenshoe, NEQ. QMMO15503; d–f, c. 10 mls E of Ravenshoe, on Palmerston Hwy, NEQ. AMC142490. a–d, entire shell; e, apical sculpture; f, post nuclear sculpture. Scale lines as marked.

0.92–1.85 mm (mean 1.36 mm), D/U ratio 3.04–3.92 (mean 3.41). Sutures strongly impressed. Whorls shouldered above and rounded below a slightly compressed periphery. Aperture roundly lunate. Lip simple, weakly thickened and twisted at the columella and slightly detached in larger individuals. Parietal callus well developed. Colour yellow-brown with darker brown zig-zag suffusions arranged in a radial pattern, continuous on base. Based on 19 measured adults.

Genitalia with epiphallus (Fig. 42a) short, muscular, forming a half loop around the penial retractor muscle before entering penis sub-apically through a simple pore (Fig. 42b). Penial retractor muscle long, inserted adjacent to the penis/epiphallus junction (Fig. 42e). Penis (Fig. 42e) pear-shaped, internally with epiphallic entrance surrounded by two spongy pilasters; a muscular collar separating the apical bulb from the lower chamber; and two flattened, fleshy pilasters lower down.

Central and lateral teeth of radula (Fig. 41d,g) typical.

Based on 8 dissected specimens (AMC150089, AMC150088, QMMO11346).

Range and Habitat

S. monteithi inhabits the humid tropical region of north Queensland between Tully and Shiptons Flat, south of Cooktown. It is found from near sea level to the mountain summits where vegetation varies from complex mesophyll vine forest to cool subtropical notophyll vine forest and montane microphyll vine fern thicket. *S. monteithi* is well represented in museum collections but its distribution is still inadequately known on the Atherton Tableland and towards the southern end of its range. Further field work should concentrate on establishing the degree of sympatry with *Setomedea* sp. The microhabitat of *S. monteithi* is similar to that of *S. seticostata* i.e. in moist rotting logs and moist accumulated forest debris.

Remarks

The penis (Fig. 42e) shows some similarity to that of *S. seticostata* in having an apical bulb with verge-like pilaster, muscular collar and lower chamber with fleshy longitudinal pilasters.

Setomedea sp.
(Figs 43–44)

Material

Lake Barrine, Atherton Tableland, rainforest (1, QMMO17163, 8 Oct 1980, G.B. Monteith); Majors Mtn, 7km SE of Ravenshoe, 1000–1100 m (1, QMMO15503, 4 May 1983, G.B. Monteith, D. Yeates); c. 10 mls E of Ravenshoe, on Palmerston Hwy, under fallen timber in rainforest (1, AMC142490, 28 Dec 1979, I. Loch, J. Farquharson).

Remarks

Compared with *S. monteithi* the shells of *Setomedea* sp. have a larger number of ribs, smaller umbilicus (diameter 0.72 mm), less elevated spire (spire protrusion 0.17 mm) and overall smaller shell with diameter 3.62 mm and height 2.13 mm (based on QMMO15503).

While this species is not formally described at this time, it is listed in order to assist with the biogeographical discussion. The reasons for the narrow distribution of *Setomedea* sp. on the western edge of the Atherton Tableland are not clear. However, this region does appear to have status as a refugium of unusual nature. The primitive camaenid land snail, *Craterodiscus pricei* McMichael, 1959 and the New Guinea related dasyurid mammal *Antechinus leo* Van Dyck, 1982, are two examples of animals with small circumscribed distributions in this area.

Gyrocochlea Hedley 1924

Gyrocochlea Hedley, 1924 (part), p. 215; Iredale, 1937a (part), p. 322; Iredale, 1941a (part), pp. 267ff; Kershaw, 1955, p. 29; Burch, 1976, p.132.

Type Species

Helix vinitincta Cox, 1868; by original designation.

Previous Studies

Gyrocochlea originally included several east-coast charopids characterised by a shell with sunken spire, wide umbilicus, "smooth" protoconch and prominent crowded radial ribs, plus *Helix stroudensis* Cox, 1864 which has an exsert spire and closed umbilicus. Iredale (1937a) added an additional four species and (1941a) removed *H. stroudensis*. Currently 14 species are included (Burch, 1976). Anatomical studies of seven species show *Gyrocochlea* to be polyphyletic. *Gyrocochlea* is restricted to *G. vinitincta* (Cox, 1868), *G. convoluta* Hedley, 1924, *G. curtisiana* (Hedley, 1912) and *G. paucilamellata* sp. nov. *'Gyrocochlea' omicron* (Pfeiffer, 1851) belongs in *Nautiliropa* gen.

nov.; '*Gyrocochlea*' *recava* (Hedley, 1912) and '*Gyrocochlea*' *concinna* Hedley, 1924 are placed in *Biomphalopa* gen. nov.

DIAGNOSIS

Adult shell diameter 4.71–8.57 mm, with 4 1/8 to 4 3/4 tightly to moderately tightly (*curtisiana*) coiled whorls, last descending more rapidly. Apex and early spire strongly to weakly (*curtisiana*) concave. Protoconch of 1 3/8 to 1 5/8 whorls. Apical sculpture of fine crowded spiral cords and numerous similarly spaced, weakly curved radial ribs forming fine beads at their intersection, or more widely spaced spiral cords and weakly curved, radial ribs which are partially fused and worn, giving the apex a pitted appearance (*curtisiana*). Post-nuclear sculpture of crowded (*vinitincta*, *curtisiana*), moderately spaced (*convoluta*) or widely spaced (*paucilamellata*), prominent, weakly protractively sinuated radial ribs. Microsculpture of numerous radial riblets and more crowded microspiral cords which "buttress" the microradials. Microspirals continuous on the major radials. Umbilicus wide, U-shaped, or V-shaped (*curtisiana*). Sutures deeply impressed. Whorls rounded below, and strongly to weakly (*curtisiana*) shouldered above a weakly rounded (*curtisiana*) to flattened periphery. Aperture ovately lunate. Lip simple. Colour light-yellow horn to dark reddish-brown, occasionally (*curtisiana*) with red flammulations.

Animal with long, slender foot, often darkly pigmented. Pallial cavity with bold black speckling on the pallial roof. Kidney with elongate pericardial lobe and rectal lobe reduced. Ovotestis oriented at right angles (*vinitincta*) or parallel to the plane of coiling. Male genitalia with long coiled epiphallus and long tubular penis with sheath. Epiphallus entering penis subapically through a conical verge (*vinitincta*) or simple pore. Terminal portion of epiphallus connected to the penis sheath by fine connective strands. Penis internally with large longitudinal pilasters and with, or without (*vinitincta*), smaller crowded pilasters near and above the epiphallic pore. Female genitalia with long vagina and shorter free oviduct. Radula without unusual features.

DISTRIBUTION AND ECOLOGY

Gyrocochlea inhabits dry to humid subtropical vine forests of the McPherson Ranges, SEQ, the Big Scrub area northern NSW, and humid notophyll vine forest and adjacent drier microphyll vine forest of the Burnett - Many Peaks - Calliope Ranges area of southern Queensland. *Gyrocochlea* prefers to live under logs.

PATTERNS OF VARIATION

Species of *Gyrocochlea* are remarkably conservative with regard to shell features differing only in size and intensity of radial ribbing except for *G. curtisiana* which has a less sunken spire, modified apical sculpture, more ribs/mm on the adult whorls, less crowded microsculpture, more rounded whorl contour and V-shaped umbilicus. The pitted apex in *G. curtisiana* is derivable by partial fusion and reduction in height of the equal spiral-radial elements. The same effect is seen in some unrelated northern Australian (Solem, 1984) and New Guinean (Solem, 1970) genera.

Anatomically *Gyrocochlea* is equally conservative. There is some difference in length of reproductive organs and minor changes in the penial pilasters. Only *G. vinitincta* differs dramatically in having a conical verge and no pustular zone apicad of the epiphallic entrance, probably because of its sympatry with *G. paucilamellata*. *G. vinitincta* has the two lobes or the ovotestis at right angles to the plane of coiling but not in the same plane as is seen in *Ngairea*, *Oreokera*, and *Hedleyoconcha*. The lobes are situated at the apical and basal margins of the whorl rather than centrally. This positional change is just a different way of dealing with space changes brought about by size increase.

Conservatism in anatomy is probably related to the small, mainly allopatric ranges of individual species which minimise interspecific interactions.

COMPARISONS

Conchologically *Gyrocochlea* is most similar to *Nautiliropa* with which it is sympatric in the eastern McPherson Ranges on the NSW/QLD border. Both genera have biconcave shells and prominent postnuclear radials but differ in sculpture and coiling pattern. In the McPherson Ranges species of *Gyrocochlea* have apical sculpture of raised spiral cords and radial ribs in a crowded, reticulate pattern producing a beaded appearance (Figs 45c, 48c, 51c), adult sculpture of major ribs which are formed from several minor ribs and lacking a periostracal blade (Figs 45f, 48f, 51f), and a body whorl which descends rapidly in front (Figs 45c, 48c, 51c). On the other hand *Nautiliropa* has apical sculpture of regularly arranged pits (Fig. 63d), adult sculpture of prominent radial ribs which are formed by expansion of a single minor rib and with a high periostracal blade (Fig. 63e), and a body whorl which does not descend (Fig. 64f). Anatomically the elongate genitalia, tubular, sheathed penis and longitudinal penial pilasters of *Gyrocochlea* contrast with the compact genitalia, pear-shaped, sheathless penis and complex pilaster arrangement of *Nautiliropa*.

KEY TO SPECIES OF *GYROCOCHLEA*

1. Apical sculpture beaded 2

   Apical sculpture of regularly arranged pits (Fig. 54e) .... *curtisiana*

2. Post nuclear sculpture of crowded ribs (Fig. 45a); shell larger (mean diameter > 7.00 mm) .... *vinitincta*

   Post nuclear sculpture of more widely spaced ribs; shell smaller (mean diameter < 7.00 mm) 3

3. Ribs on body whorl very widely spaced (Fig. 49a); mean ribs/mm 1.96 ..... *paucilamellata*

   Ribs on body whorl moderately spaced (Fig. 48a); mean ribs/mm 3.92 .... *convoluta*

Gyrocochlea vinitincta (Cox, 1868) (Figs 45–47; Tables 11,12)

Helix vinitincta Cox, 1868, p. 18, pl. 1, figs 6, 6a.
Diplomphalus vinitinctus (Cox); Tryon, 1885, p. 115, pl. 24, figs 88,89.
Monomphalus vinitinctus (Cox); Ancey, 1888, p. 359.
Endodonta vinitincta (Cox); Shirley, 1921, p. 34.
Gyrocochlea vinitincta (Cox); Hedley, 1924, p. 218, pl. 31, figs 28–31; Iredale, 1937a, p. 322; Iredale, 1941a, p.268, fig. 6; Kershaw, 1956a, p. 138.

COMPARISONS

The large size, simple sutures, beaded apical sculpture, and strongly depressed spire differentiate this species from the sympatric *Elsothera genithecata*, which has a flat to slightly elevated spire with strong curved radial ribs on the apex, channelled sutures and very inflated body whorl. *G. vinitincta* can be distinguished from *G. paucilamellata*, and *G. convoluta* by its larger size and more numerous radial ribs. *Nautiliropa omicron* has the general shell form of *G. vinitincta* but is smaller, with greater number of ribs/mm, body whorl that does not descend, and flammulated shell.

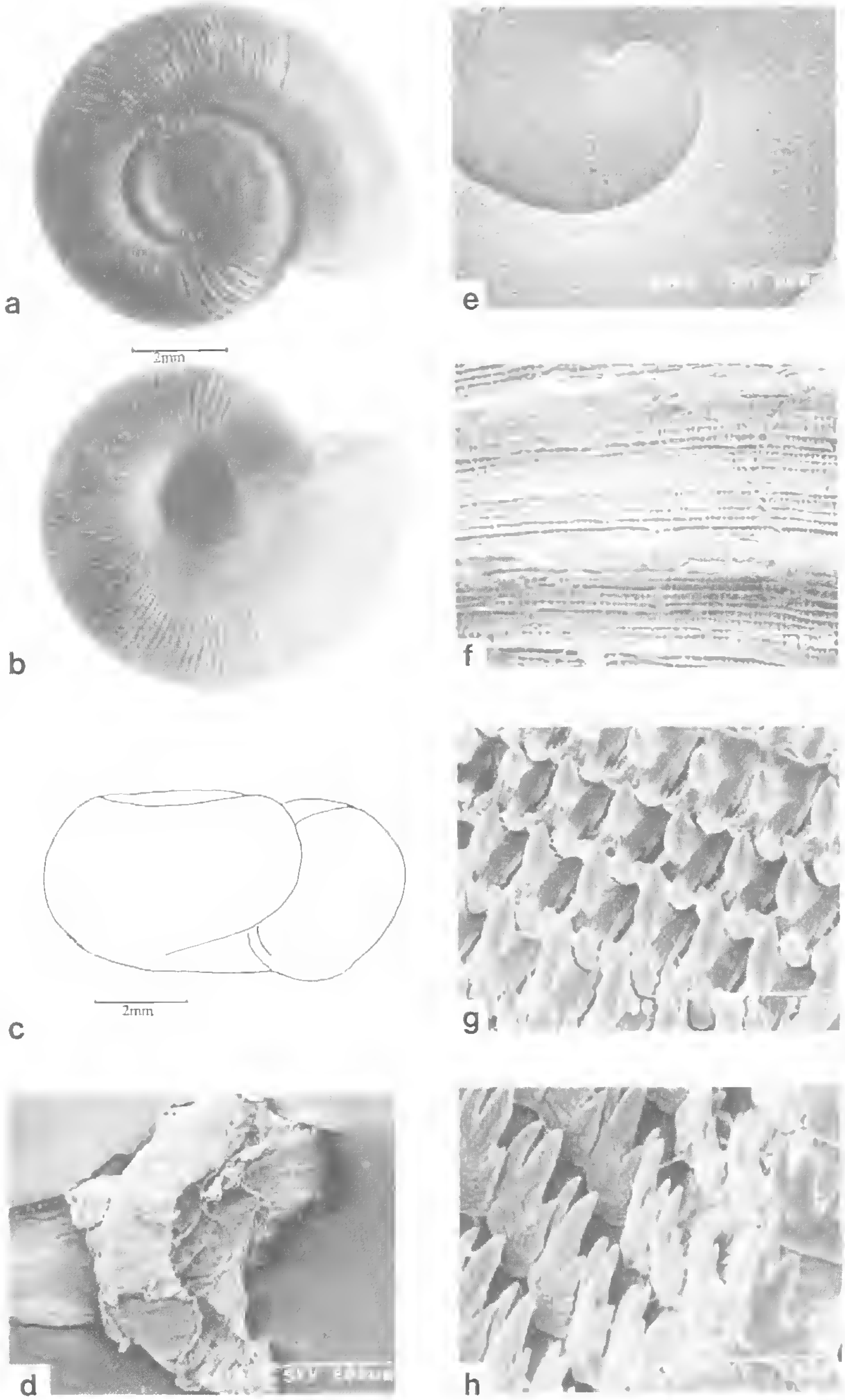
TYPE MATERIAL

HOLOTYPE: AMC63490, Upper Richmond River, NSW. Height of shell 4.87 mm, diameter 7.98 mm, H/D ratio 0.61, D/U ratio 3.99, whorls 4 1/2+.
PARATYPE: AMC103624, same data as holotype.

OTHER MATERIAL

Richmond River, NSW (5, AMC139754; 3, AMC139769, Petterd, ex Cox); Byron Bay, NSW (5, AMC139753, S.W. Jackson); Big Scrub, Murwillumbah, NSW (1, AMC63837, Lower, ex Cox); Lismore, NSW (2, AMC139752, ex C. McLauchlan, Bent Coll); Red Scrub Flora Reserve, Whian Whian S.F., NSW (28°38'S, 153°19'E), 210 m (3, AMC139751, 15 May 1976, P.H. Colman, I. Loch); Terania Creek, NSW (28°34'S, 153°19'E), (3, AMC153725, 16 May 1976, P.H. Colman, I. Loch); Mt. Warning N.P., NSW (28°24'S, 153°16'E) NVF/Palms (2, QMMO10487, Mar 1981, AM/QM-ABRS; 2, QMMO12735, AMC136830, 15 Dec 1981, AM/QM-ABRS). Upper Tallebudgera Ck, SEQ, 600 m (2, QMMO15990, 9 Dec 1984, G.B. Monteith); Warrie Circuit, Springbrook N.P., SEQ, CNVF, under log in litter (1, QMMO16902, 6 Apr 1986, J. Stanisic); c. 1.6 km N of Numinbah Valley Turnoff, on Burleigh-Springbrook Rd, SEQ, NVF/Palms, litter (2, QMMO17319, 17 Dec 1980, J. Stanisic); Natural Bridge N.P., SEQ (28°13'S, 153°14'E), CNVF (1, QMMO6281, Oct 1976, M.J. Bishop).

LAMINGTON N.P., SEQ: Border Track, near O'Reillys NVF, under logs (3, QMMO16875, 31 Mar 1984, J. Stanisic); Orchid Bower, Binna Burra, NVF, under stone (1, QMMO16864, 19 Apr 1986, J. Stanisic, J. Chaseling); Tullawallal Circuit, Binna Burra, NVF, under logs (7, QMMO16739, 2 Oct 1985, J. Stanisic, D. Potter, J. Chaseling); Border Track, Binna Burra, NVF, under log (3, QMMO16869, 10 Mar 1984, J. Stanisic); Araucaria Track, Binna Burra, NVF, under logs (1, QMMO16864, 19 Apr 1986, J. Stanisic, J. Chaseling); Tullawallal Circuit, Binna Burra, NVF, under logs (7, QMMO16739, 2 Oct 1985, J. Stanisic, D. Potter, J. Chaseling); Border Track, Binna Burra, NVF, under log (3, QMMO16869, 10 Mar 1984, J. Stanisic); Araucaria Track, NVF, under logs (3, QMMO16579, 27 Sept 1986, J. Stanisic); O'Reillys (28°14'S, 153°15'E) MFF (3, QMMO10431, 17 Mar 1981, AM/QM-ABRS); Binna Burra (28°13'S, 153°12'E) 850 m, CNVF (1, QMMO6078, Apr 1976, M.J. Bishop).


a
2mm
b
2mm
c
d
e
f
g
h

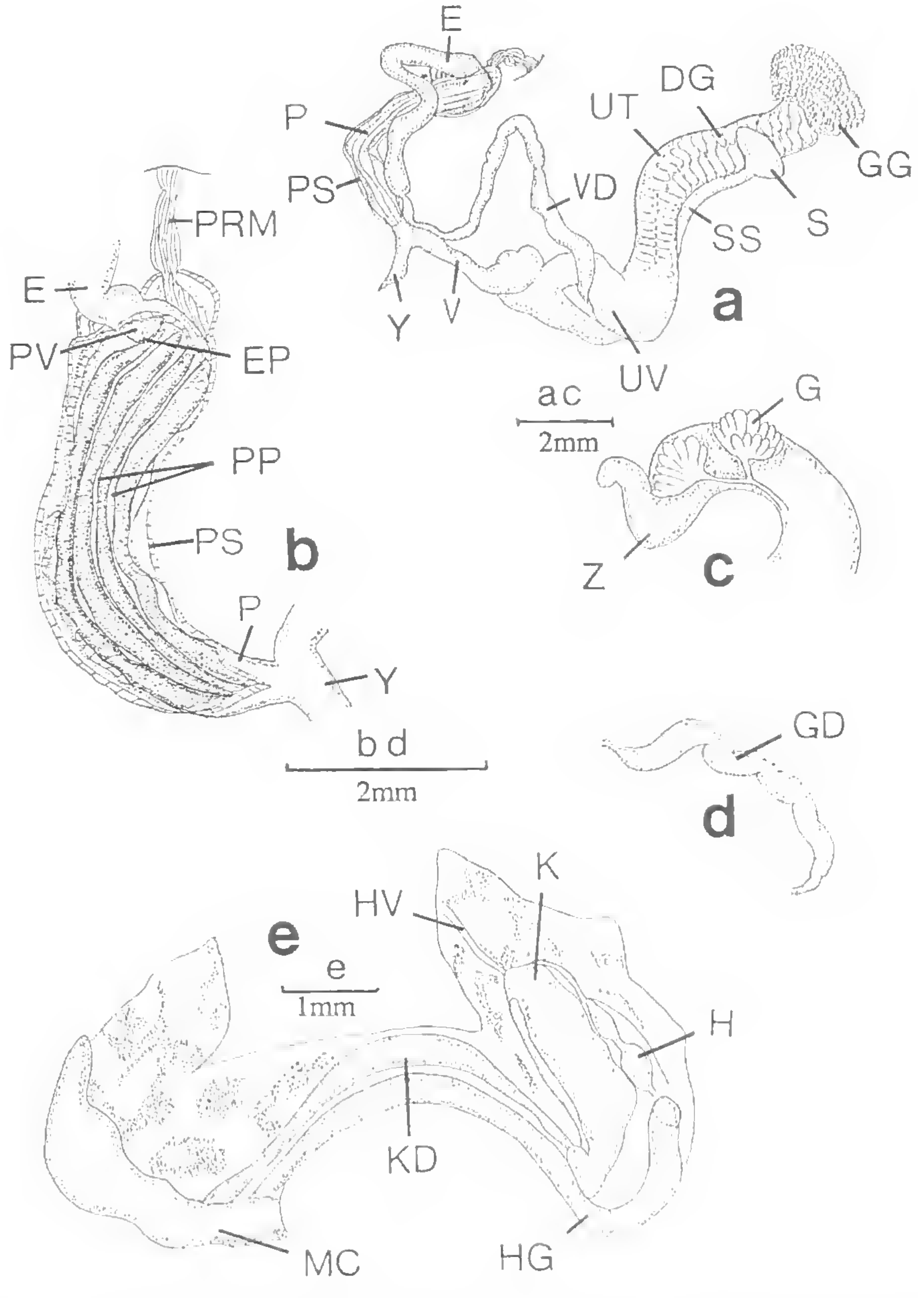


FIG. 46. *Gyrocochlea vinitincta* (Cox, 1868). Mt Warning N.P., NSW. QMMO12735. a, genitalia; b, penis interior; c, ovotestis; d, hermaphroditic duct; e, pallial cavity. Scale lines as marked.

FIG. 45. *Gyrocochlea vinitincta* (Cox, 1868). a–c, Upper Richmond R. NSW. AMC63490, holotype; d, g–h, c. 1.6km N of Numinbah Valley turnoff, on Burleigh-Springbrook Rd, SEQ. QMMO17319; e–f, O'Reillys, Lamington N.P., SEQ. QMMO10431. a–c, entire shell; d, jaw; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale lines as marked.

TABLE 11. RANGE OF VARIATION IN *GYROCOCHLEA*, *NAUTILIROPA*, *BIOMPHALOPA* AND *LETOMOLA* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Gyrocochlea vinitincta	6	4 3/8+ (4 1/4+ to 4 5/8)	4.52 (3.95–4.87)	7.91 (7.22–8.57)	0.57 (0.53–0.63)		3.50 (3.11–3.69)	---	118.83 (106–153)	4.77 (4.22–5.68)	2.00 (1.79–2.26)	3.97 (3.46–4.32)
Gyrocochlea convoluta	4	4 5/8+ (4 1/2 to 4 3/4)	3.36 (3.03–3.78)	5.78 (5.46–6.05)	0.58 (0.55–0.63)		2.65 (2.35–2.94)	---	71.5 (58–83)	3.92 (3.26–4.36)	1.70 (1.62–1.87)	3.40 (3.14–3.55)
Gyrocochlea paucilamellata	3	4 1/2 (4 1/4 to 4 5/8)	3.31 (3.19–3.45)	5.35 (5.04–5.55)	0.62 (0.58–0.65)	...	2.46 (2.35–2.52)		32.7 (27–40)	1.96 (1.57–2.52)	1.65 (1.49–1.75)	3.25 (3.13–3.38)
Gyrocochlea cuesiana	17	4 1/2- (4 1/8–4 3/4)	2.84 (2.52–3.28)	5.38 (4.71–5.97)	0.53 (0.47–0.65)	0.08	2.07 (1.85–2.61)	0.04 (0.04–0.05)	125.82 (93–159)	7.42 (6.13–9.12)	1.69 (1.45–1.92)	3.23 (2.76–3.52)
Nautiliropa omicron	11	4 3/8+ (4–4 5/8+)	2.82 (2.35–3.11)	5.24 (4.20–5.97)	0.54 (0.48–0.57)		2.17 (1.85–2.52)	---	113.6 (72–167)	6.90 (5.02–9.79)	1.47 (1.23–1.64)	3.58 (2.62–4.22)
Biomphalopa recava	3	5 1/4 (5 to 5 3/8)	2.43 (2.13–2.68)	4.49 (4.17–4.69)	0.54 (0.51–0.58)	-	1.79 (1.66–1.87)	---	91.67 (81–100)	6.67 (6.17–7.47)	1.93 (1.87–2.00)	2.32 (2.23–2.40)
Biomphalopa concinna	4	4 5/8+ (4 1/8–5 1/8)	1.71 (1.58–1.87)	3.08 (2.64–3.45)	0.56 (0.53–0.60)		1.37 (1.19–1.53)	---	84.8 (80–95)	8.82 (7.84–9.63)	1.19 (1.03–1.27)	2.58 (2.28–2.80)
Letomola contortus	13	3 7/8- (3 1/2–4+)	0.91 (0.80–1.03)	2.05 (1.81–2.24)	0.45 (0.40–0.51)		0.69 (0.64–0.76)		...	–	0.77 (0.64–0.86)	2.68 (2.42–3.03)

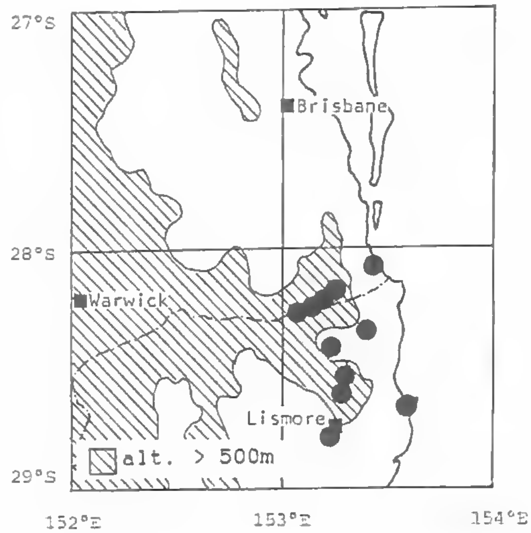


FIG 47. Distribution of *Gyrocochlea vinitincta* (Cox, 1868).

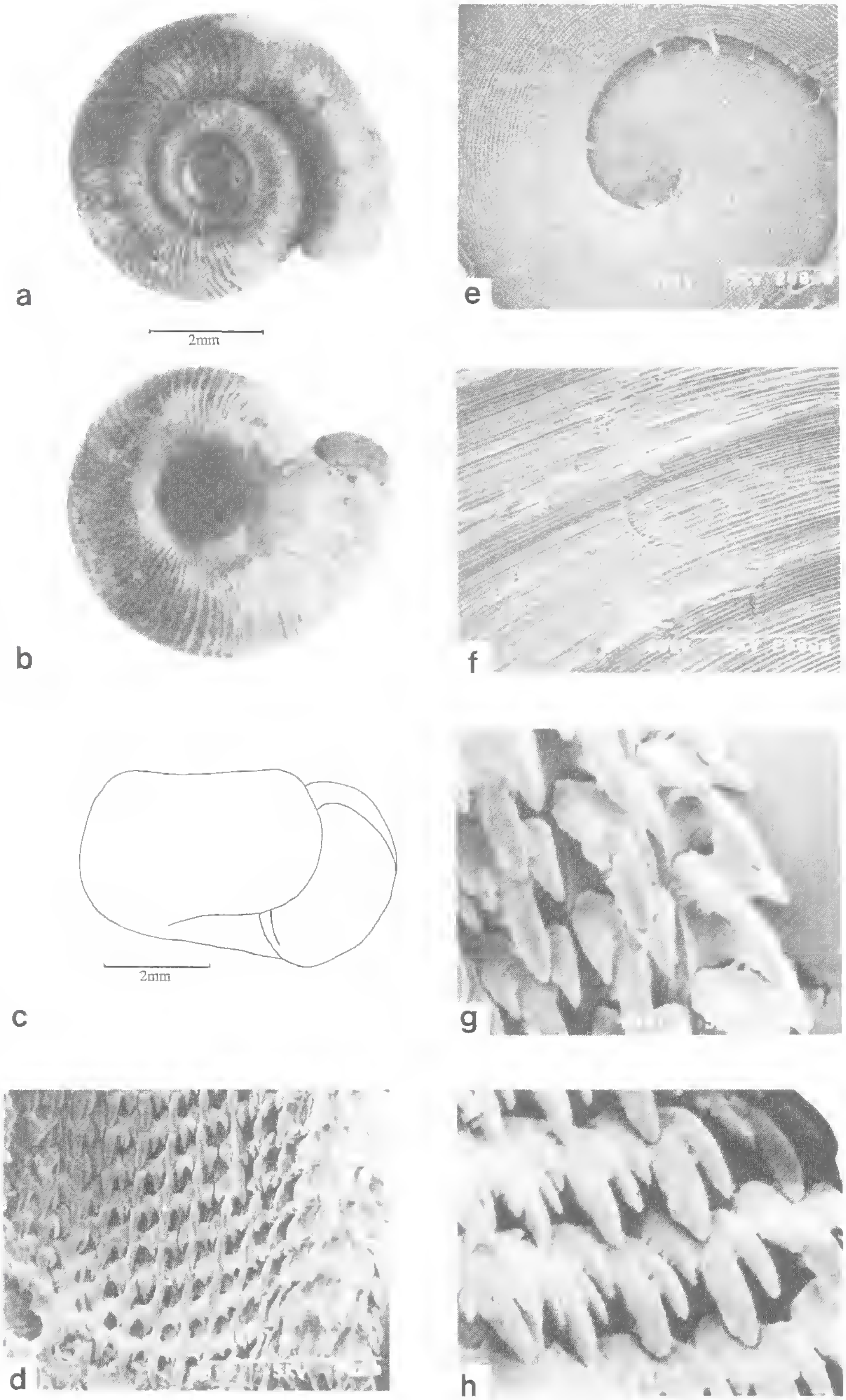
DIAGNOSIS

Shell diameter 7.22–8.57 mm (mean 7.91 mm), with 4 1/4+ to 4 5/8 (mean 4 3/8+), tightly coiled whorls, last descending more rapidly. Apex and early spire (Fig. 45a) strongly concave, height of shell 3.95–4.87 mm (mean 4.52 mm). H/D ratio 0.53–0.63 (mean 0.57). Protoconch of 1 1/2 to 1 3/4 whorls, mean diameter 896.7 μm at 1 1/2 whorls. Apical sculpture (Fig. 45e) of fine, crowded spiral cords and numerous, weakly curved radial ribs, which are raised at their intersection with the spiral cords creating a beaded effect. Post nuclear sculpture (Fig. 45f) of numerous, high, crowded, protractively sinuated radial ribs, 106–153 (mean 118.8) ribs on the body whorl. Ribs/mm 4.22–5.68 (mean 4.77). Microsculpture (Fig. 45f) of fine radial riblets, 6–12 between each pair of major ribs, continuing onto the sides of the major ribs, and numerous fine microspiral cords which are not raised at their junction with the microradials. Umbilicus (Fig. 45b) relatively wide, U-shaped, diameter 1.79–2.26 mm (mean 2.00 mm). D/U ratio 3.46–4.32 (mean 3.97). Sutures (Fig. 45a) weakly impressed, becoming deeper on the body whorl. Whorls rounded below and strongly shouldered above a weakly compressed periphery. Aperture ovately lunate. Lip simple, columella not expanded. Parietal callus developed. Colour yellow-brown to dark reddish-brown. Based on 6 measured specimens.

Genitalia with ovotestis (Fig. 46c) oriented at

TABLE 12 - LOCAL VARIATION IN *GYROCOCHLEA VINITINCTA* (COX, 1868), *GYROCOCHLEA CONVOLUTA* HEDLEY, 1924, *GYROCOCHLEA PAUCILAMELLATA* SP. NOV. AND *GYROCOCHLEA CURTISIANA* (HEDLEY, 1912) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Gyrocochlea vinitincta												
Richmond River AMC 63490 (Holotype)	1	4 1/2+	4.87	7.98	0.61	---	3.53	---	106	4.22	2.00	3.99
AMC 103624	1	4 5/8	4.62	8.57	0.54	---	3.61	---	153	5.68	2.26	3.80
Mt Warning QMMO 10487	1	4 3/8+	3.95	7.23	0.55	---	3.11	---	115	5.06	2.09	3.46
Tallebudgera Creek QMMO 15990	2	4 1/2- (4 1/4+to 4 5/8)	4.66±0.210 (4.45–4.87)	8.07±0.336 (7.73–8.40)	0.58±0.05 (0.53–0.63)	---	3.57±0.126 (3.45–3.70)	---	112.5±5.5 (107–118)	4.44±0.04 (4.40–4.47)	1.83±0.043 (1.79–2.00)	4.26±0.06 (4.20–4.32)
Binna Burra QMMO 16579	1	4 1/4+	4.37	7.56	0.58	---	3.61	---	114	4.79	1.87	4.04
Gyrocochlea convoluta												
Beaudesert AMC 5815 (Holotype)	1	4 5/8	3.36	5.88	0.57	---	2.69	---	75	4.05	1.87	3.14
Toonumbar QMMO 10927	1	4 3/4	3.78	6.05	0.63	---	2.94	---	83	4.36	1.70	3.55
Mt Lindesay AMC 139750	1	4 3/4	3.03	5.46	0.55	---	2.35	---	58	3.38	1.62	3.38
Richmond Range QMMO 10970	1	4 1/2-	3.28	5.71	0.57	---	2.61	---	70	3.90	1.62	3.53
Gyrocochlea paucilamellata												
Upper Pine Creek QMMO 17321 (Holotype)	1	4 5/8	3.19	5.55	0.58	---	2.52	---	31	1.78	1.70	3.25
QMMO 16546	1	4 1/2-	3.45	5.46	0.63	---	2.52	---	27	1.57	1.75	3.13
Mt Tamborine QMMO 17320	1	4 1/4-	3.28	5.04	0.65	---	2.35	---	40	2.52	1.49	3.38
Gyrocochlea curtisiana												
Mt Larcom AMC 32990 (Holotype)	1	4 1/4	2.52	5.29	0.48	---	1.93	---	109	6.55	1.53	3.45
Bobby Range QMMO 16860	3	4 1/2- (4 1/8–4 3/4)	2.92±0.210 (2.52–3.28)	5.13±0.270 (4.71–5.63)	0.58±0.037 (0.54–0.65)	0.08	1.96±0.074 (1.85–2.10)	0.04±0.003 (0.04–0.05)	110.0±11.2 (93–131)	6.79±0.327 (6.28–7.40)	1.69±0.086 (1.53–1.83)	3.03±0.037 (2.96–3.07)
QMMO 14716	1	4 5/8+	3.03	5.63	0.54	---	2.61	---	115	6.50	1.79	3.15
Dawes Range QMMO 12642	7	4 1/2- (4 1/4-to4 3/4)	2.85±0.087 (2.52–3.19)	5.41±0.124 (4.96–5.97)	0.53±0.009 (0.51–0.58)	---	2.05±0.051 (1.85–2.27)	---	128.6±9.31 (102–159)	7.52±0.416 (6.13–9.12)	1.66±0.058 (1.45–1.92)	3.37±0.056 (3.17–3.52)


a
2mm
b
2mm
c
d
e
f
g
h

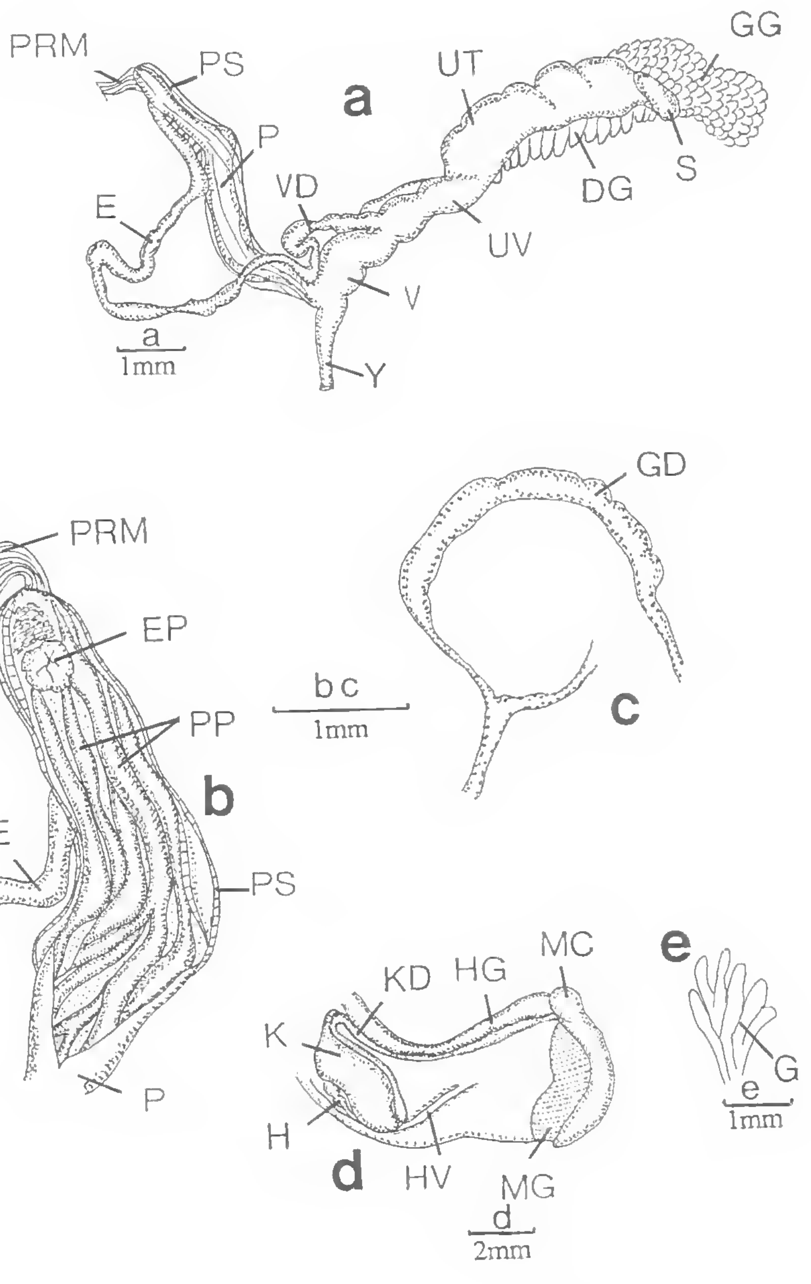


FIG 49. *Gyrocochlea convoluta* Hedley, 1924. Along tributary of Iron Pot Ck, 1km N of Toonumbar, NSW. QMMO10927. a, genitalia; b, penis interior; c, hermaphroditic duct; d, pallial cavity; e, ovotestis clump. Scale lines as marked.

FIG 48. *Gyrocochlea convoluta* Hedley, 1924. a–c, Beaudesert, Qld. AMC5815, holotype; d, g–h, Along tributary of Iron Pot Creek, 1km N of Toonumbar, NSW. QMMO10927; e–f, Mt Lindesay, Richmond R, NSW. AMC39750. a–c, entire shell; d, lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, cusp angles on lateral teeth; h, lateromarginal and marginal teeth. Scale lines as marked.

right angles to the plane of coiling, one clump on the apex and one on the base of the whorl and directed toward each other. Epiphallus (Fig. 46b) kinked and entering the penis subapically through a conical verge (Fig. 46b). Penis (Fig. 46b) a long, slender, muscularised tube covered with a thin penis sheath. Upper portion of the epiphallus connected to penis sheath by short fibres (Fig. 46a). Internally the penis has several longitudinal spongy thickenings (Fig. 46b).

Radula without unusual features.

Based on 2 dissected adults (QMMO12735).

RANGE AND HABITAT

G. vinitincta occurs in the Big Scrub area of northern NSW, the eastern McPherson Ranges, SEQ, and some adjacent mountains and valleys of the Scenic Rim. It prefers cool to warm subtropical notophyll vine forests and does not inhabit adjacent drier vine forests with *Araucaria* emergents. Specimens have been taken from under logs and under stones, often in pairs.

REMARKS

G. vinitincta and *G. paucilamellata* are sympatric in parts of the Lamington Plateau, SEQ, and the structural differences in their penes probably provide species recognition features for the snails.

Gyrocochlea convoluta Hedley, 1924
(Figs 48–50; Tables 11, 12)

Gyrocochlea convoluta Hedley, 1924 (part), p. 216, pl. 29, figs 7–9; Iredale, 1937a, p. 322

COMPARISONS

G. convoluta differs from *G. paucilamellata* in being slightly larger (Table 11) and in having a greater number of ribs on the body whorl. Anatomically the differences are minor. *G. convoluta* (Fig. 49b) has more irregular longitudinal pilasters in the lower part of the penial chamber and a larger pustular zone apicad of the epiphallic pore than *G. paucilamellata* (Fig. 52b). *G. convoluta* is easily distinguished from *G. vinitincta* by its smaller size and more widely spaced radial ribs, and from *Nautiliropa omicron* by its fewer radial ribs, larger umbilicus and monochrome brown shell on which the last whorl descends.

PREVIOUS STUDIES

Gyrocochlea convoluta was based on the holotype and specimens from Camerunga (= Canungra), SEQ. The latter material has not been found and efforts to collect at Canungra yielded only *G. paucilamellata*; Hedley probably had both species.

TYPE MATERIAL

HOLOTYPE: AMC5815, Beaudesert, Qld. Height of shell 3.36 mm, diameter 5.88 m, H/D ratio 0.57, D/U ratio 3.14, whorls 4 5/8.

OTHER MATERIAL

Mt. Lindesay, Upper Richmond River, NSW (3, AMC139750, 27 Apr 1958, L. Price), c. 1.7 km along McIntosh's Rd, nr Back Creek, E side of Richmond Range, NENSW (28°25'S, 152°44'E), broadleaf/sclerophyll (1, QMMO10970, 15 Mar 1981, AM/QM-ABRS); along tributary of Iron Pot Creek, 1 km N of Toonumbar, NSW (28°34'S, 152°45'E) (1, QMMO10927, Mar 1981, AM/QM-ABRS).

DIAGNOSIS

Shell large, diameter 5.46–6.05 mm (mean 5.78 mm), with 4 1/2- to 4 3/4 (mean 4 5/8+) tightly coiled whorls, last descending more rapidly. Apex and early spire (Fig. 48a) strongly concave, height of shell 3.03–3.78 mm (mean 3.36 mm). H/D ratio 0.55–0.63 (mean 0.58). Protoconch of 1 1/2 to 1 5/8+ whorls, mean diameter 785.5 µm at 1 1/2 whorls. Apical sculpture (Fig. 48e) of fine spiral cords and fine low radial thickenings, raised at their junction creating a beaded effect. Postnuclear sculpture (Fig. 48f) of numerous, widely spaced, high, strongly protractively sinuated radial ribs, 58–83 (mean 71.5) ribs on the body whorl. Ribs/mm 3.38–4.36 (mean 3.92). Microsculpture (Fig. 48f) of fine radial riblets, 18–30 between each pair of major ribs, and very fine, crowded spiral cords. Umbilicus (Fig. 48b) U-shaped, diameter 1.62–1.87 mm (mean 1.70 mm). D/U ratio 3.14–3.55 (mean 3.40). Sutures impressed, becoming deep on the last whorl. Whorls rounded below and strongly shouldered above a slightly flattened periphery (Fig. 48c). Aperture ovately lunate. Lip simple. Parietal callus developed, radially sculptured. Colour golden brown. Based on 4 measured adults.

Genitalia with epiphallus long, muscularised, bound for part of its length to the apical part of the penis (Fig. 49a), internally with longitudinal thickenings, entering penis subapically through a fleshy pore (Fig. 49b). Penis (Fig. 49b) long, tubular, without expanded apical portion, internally with thin fleshy longitudinal pilasters (Fig. 49b) which become less regular in the lower part

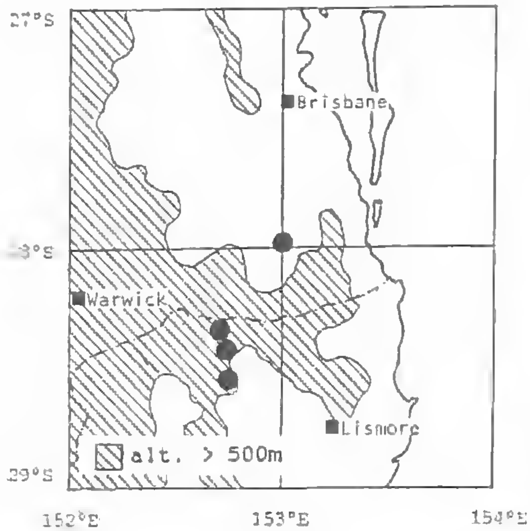


FIG 50. Distribution of *Gyrocochlea convoluta* Hedley, 1924.

of the chamber, and a small pustulose zone above the epiphallic pore. Penial retractor muscle inserting apically on the penis.

Radula (Fig. 48g, h) typical.

Based on 1 dissected specimen (QMMO-10927).

RANGE AND HABITAT

G. convoluta inhabits notophyll vine forests of the Upper Richmond Range, NSW, and gallery forests of creeks which flow from these highlands. No data is available on microhabitat although shell form suggests that it lives under logs.

REMARKS

G. convoluta is a conchologically distinctive species and differs only slightly from *G. paucilamellata* in genital anatomy.

Gyrocochlea paucilamellata sp. nov.
(Figs 51–53; Tables 11, 12)

Gyrocochlea convoluta Hedley, 1924 (part), p. 216.

ETYMOLOGY

Latin *pauci*, few; *lamella*, plate; for the sparse number of radial ribs on the adult whorls.

COMPARISONS

The brown shell, widely separated radial ribs, biconcave shell and wide umbilicus distinguish *G. paucilamellata* from its congeners and other charopids in the border ranges area. *G. vinitincta* is much larger with more numerous radial ribs (Table 11). *G. convoluta* has more than twice as many ribs on the body whorl. Anatomically *G. paucilamellata* (Fig. 52b) differs from *G. vinitincta* (Fig. 46b) by lacking a penial verge and in having an apical pustular zone in the penis. *Nautiliropa omicron*, which also is sympatric with *G. paucilamellata*, has many more radial ribs and a flammulated shell. Anatomically *N. omicron* has a penis which lacks a sheath, contains complex pilasters, and is pear-shaped (Fig. 65c).

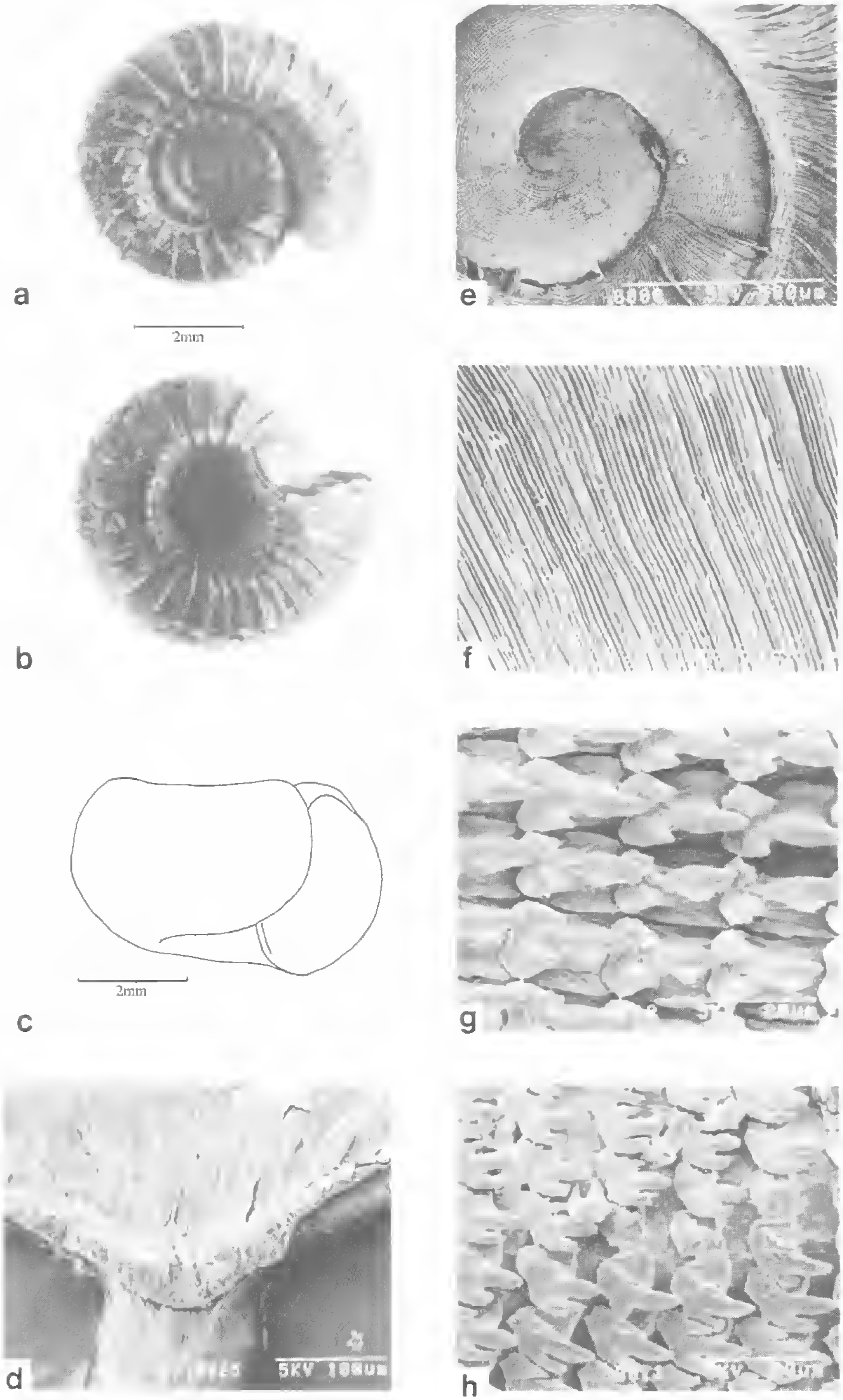
TYPE MATERIAL

HOLOTYPE: QMMO17321. Upper Pine Creek, Canungra, SEQ. NVF/*Araucaria*, under bark and logs. Collected by J. Stanisic, D. Potter, 1 Oct 1986.

PARATYPES: QMMO16546, 21 specimens, same data as holotype; Kweebani Caves Walk, Binna Burra, Lamington N.P., SEQ, NVF, under logs (1, QMMO16889, 30 Sept 1985, J. Stanisic, D. Potter, J. Chaseling); Mt Tamborine, SEQ, under bark in leaf litter (4, QMMO17320, VK 7299, 3 Nov 1979, V. Kessner); Upper Pine Creek, Canungra, SEQ, NVF/Araucaria, under log (1, QMMO16585, 29 Sept 1986, J. Stanisic, J. Chaseling).

DIAGNOSIS

Shell large for family, diameter 5.04–5.55 mm (mean 5.35 mm) with 4 1/4- to 4 5/8 (mean 4 1/2-) tightly coiled whorls. Apex and early spire (Fig. 51a) strongly concave. Height 3.19–3.45 mm (mean 3.31 mm), H/D ratio 0.58–0.65 (mean 0.62). Last whorl descending. Protoconch of 1 1/2+ to 1 5/8+ whorls, flat, mean diameter 745.3 µm at 1 1/2 whorls. Apical sculpture (Fig. 51f) finely reticulate, consisting of numerous, crowded fine spiral cords crossing numerous crowded, weakly sinuated radial ribs. Post apical sculpture (Fig. 51f) of few, bold, protractively sinuated radial ribs, 27–40 (mean 32.7) ribs on the body whorl. Ribs/mm 1.57–2.52 (mean 1.96). Microsculpture (Fig. 51f) of fine, crowded radial riblets, 30–45 between each pair of major ribs, and very fine inconspicuous spiral cords, only visible between the microradials. Umbilicus (Fig. 51b) wide, U-shaped, diameter 1.49–1.75 mm (mean 1.65 mm). D/U ratio 3.13–3.38 (mean 3.25). Sutures impressed, forming a deep furrow as the body whorl descends. Whorls rounded below and strongly shouldered above a weakly rounded periphery (Fig. 51c). Aperture ovately lunate. Lip simple. Colour deep reddish-


a
e
2mm
b
f
c
2mm
g
d
h

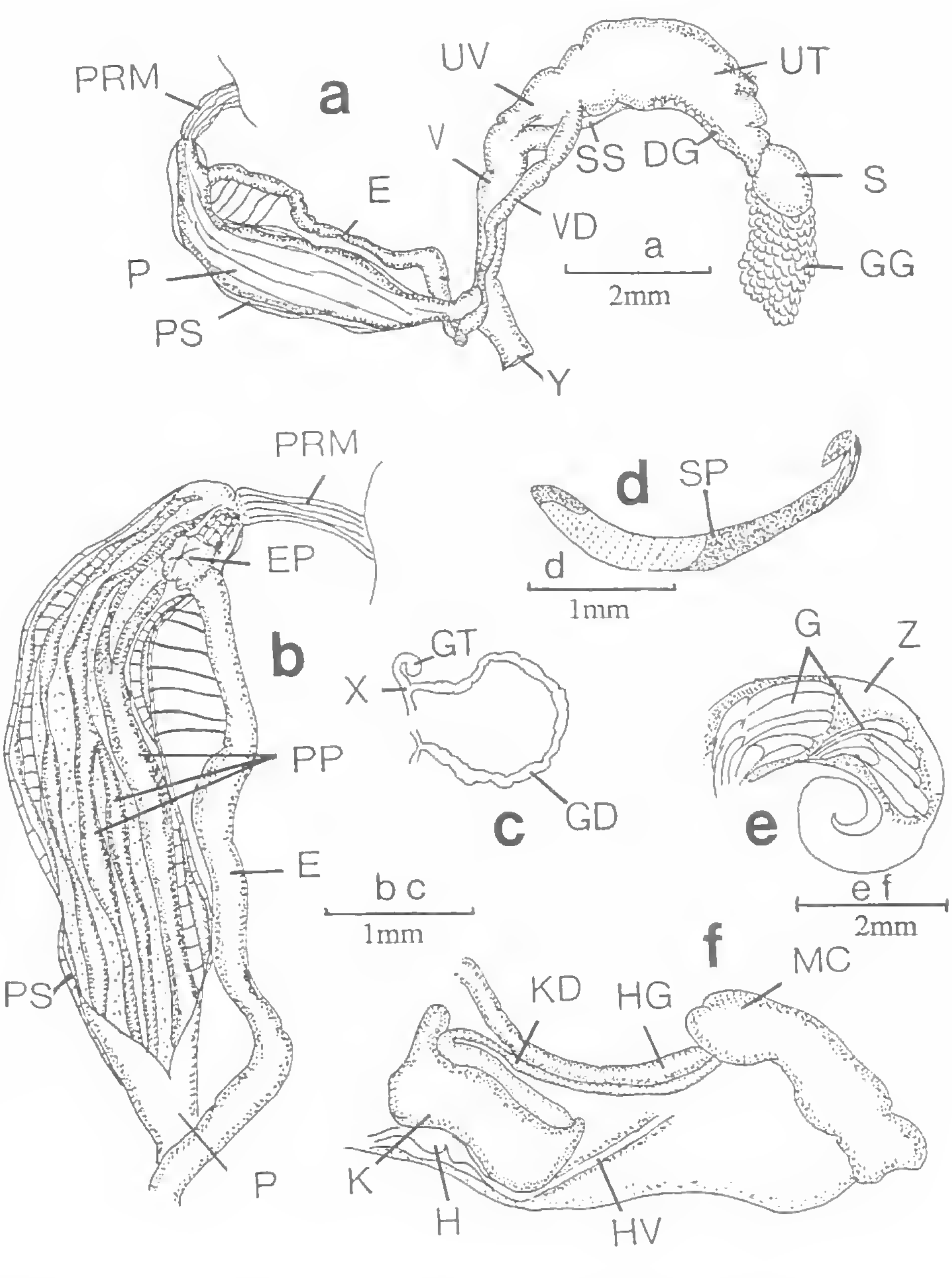


FIG. 52. *Gyrocochlea paucilamellata* sp. nov. Upper Pine Ck, Canungra, SEQ. QMMO16546, paratype. a, genitalia; b, penis interior; c, talon and hermaphroditic duct; d, spermatophore; e, ovotestis; f, pallial cavity. Scale lines as marked.

FIG. 51. *Gyrocochlea paucilamellata* sp. nov. a–c, Upper Pine Creek, Canungra, SEQ. QMMO17321, holotype; d, g–h, same data as holotype. QMMO16546, paratype; e–f, Mt Tamborine, SEQ. QMMO17320, paratype. a–c, entire shell; d, jaw; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale lines as marked.

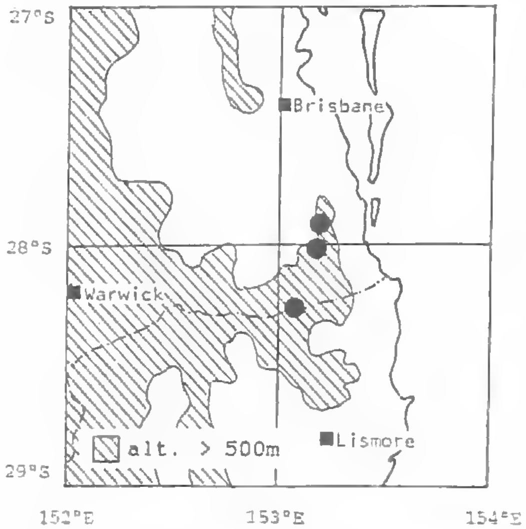


FIG 53. Distribution of *Gyrocochlea paucilamellata* sp. nov.

brown to light-yellow horn. Based on 3 measured adults.

Genitalia with epiphallus long, muscular, and strongly coiled, entering the penis subapically through a simple pore (Fig. 52b) surrounded by a fleshy collar. Epiphallus partially bound (apically) to the penis sheath. Penis (Fig. 52b) elongate, tubular, muscularised, internally with longitudinal pilasters (Fig. 52b) in a regular pattern, and smaller pilasters apicad of the epiphallic pore. Penial retractor muscle inserting apically on the penis. Spermatophore subclavate with a long recurved chitinous tail at one end (Fig. 52d).

Radula typical.

Based on 4 dissected specimens (QMMO-16546).

RANGE AND HABITAT

G. paucilamellata occurs in the eastern part of the Lamington Plateau, SEQ, and in the Darlington-Canungra Range area as far north as Mt Tamborine, SEQ in cool subtropical to warm subtropical notophyll vine forest, sometimes with *Araucaria* emergents (Upper Pine Creek, SEQ). The species has been collected from under fallen bark and logs. In spite of relatively concentrated collecting in the Lamington Plateau area, it has been found there only once.

REMARKS

G. paucilamellata has a distribution quite distinct from that of *G. convoluta* and is geographically isolated from it by the Albert River Valley.

Gyrocochlea curtisiana (Hedley, 1912)
(Figs 54–56; 64a-c; Tables 11, 12)

Endodonta iuloidea var. *curtisiana* Hedley, 1912, p. 264, pl. 9, figs 49–51.

Gyrocochlea curtisiana (Hedley); Iredale, 1937a, p. 323.

COMPARISONS

G. curtisiana is distinguished in the genus by its almost flat spire, apical sculpture of regularly arranged pits, often flammulated shell and large number of ribs on the body whorl. *Nautiliropa omicron* has apical sculpture of regularly arranged pits, flammulated shell and large number of ribs on the body whorl, but has a very depressed spire and a body whorl which does not descend.

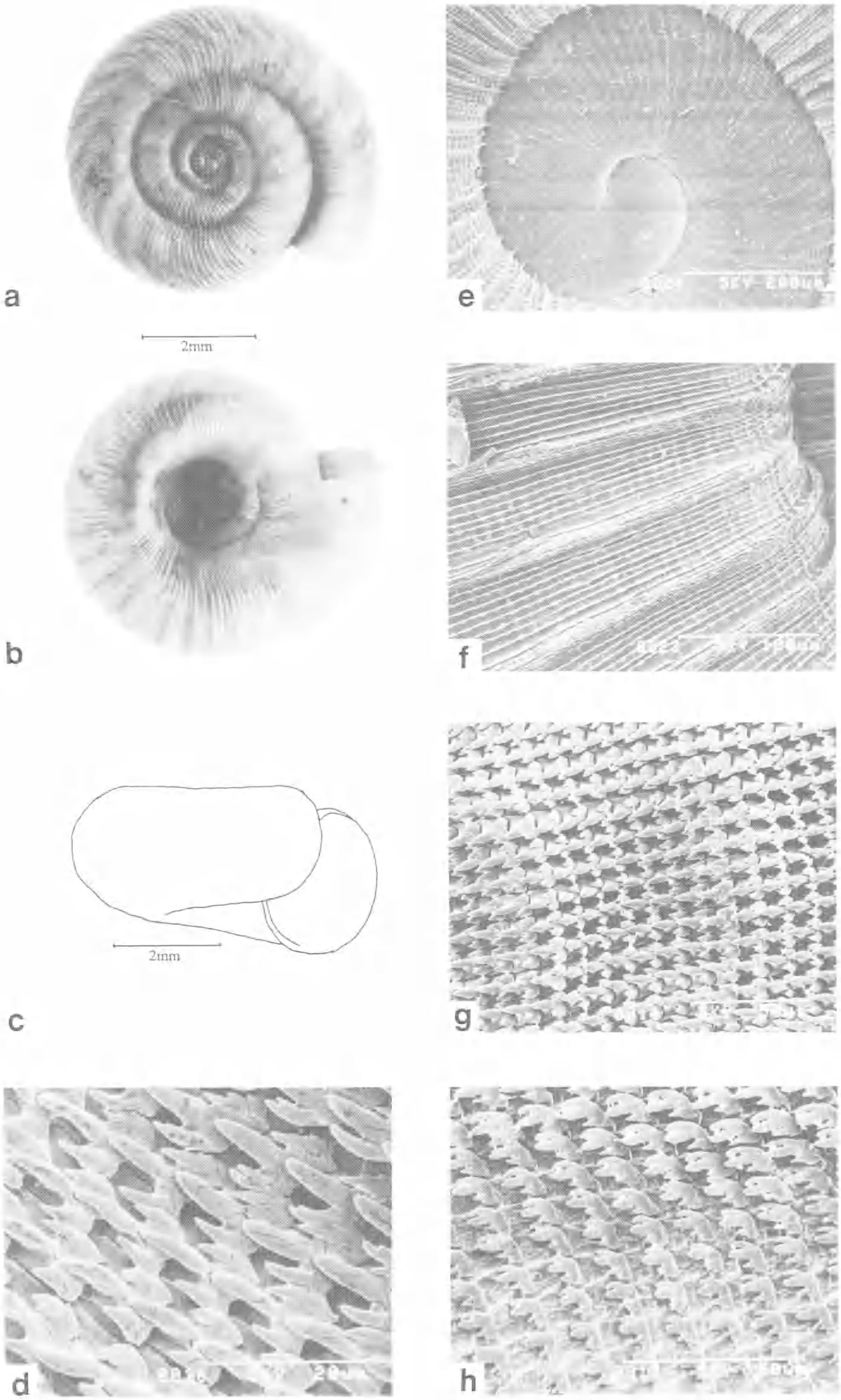
PREVIOUS STUDIES

Hedley (1912) described *G. curtisiana* as a variety of *'Helix' iuloidea* Forbes, 1851 from Port Molle, Central Queensland, following comparison of specimens with the type of *H. iuloidea* by E.A. Smith (Hedley, 1912, p. 265). Hedley (in Hedley and Musson, 1892) had included this variety with *'Charopa' omicron* (Pfeiffer, 1851). The two species are similar in shell appearance but are anatomically distinct. Hedley (1924) listed a large number of species under *'Gyrocochlea'* without including his new variety but recorded *'Gyrocochlea' omicron* as having a distribution as far north as Miriam Vale, SEQ. There is little doubt that these early published records of *'G'. omicron* from the Miriam Vale area were based on specimens of *G. curtisiana*.

TYPE MATERIAL

HOLOTYPE: AMC32990, "found under log in forest just outside Springs Scrub", Mt Larcom, Port Curtis, SEQ. Collected by S.W. Jackson, Aug 1908. Height

FIG 54. *Gyrocochlea curtisiana* (Hedley, 1912). a–c, Granite Creek, foothills of Bobby Range, SEQ. QMMO14716; d–h, Kroombit Tops, SEQ. QMMO16517, QMMO16453. a–c, entire shell; d, central and lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale line as marked.


a
e
2mm
b
f
2mm
c
g
d
h

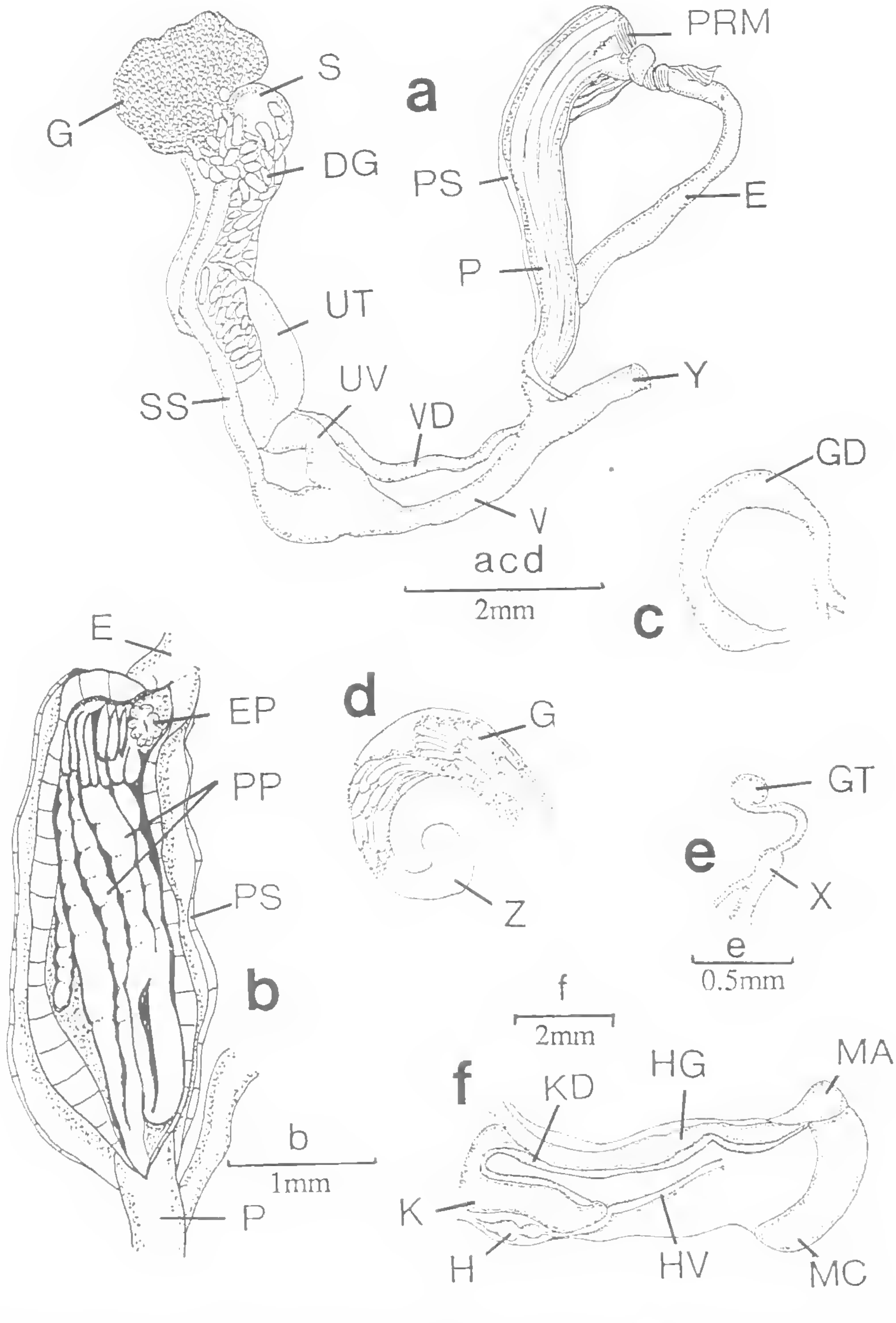


FIG 55. *Gyrocochlea curtisiana* (Hedley, 1912). Kroombit Tops, SEQ. QMMO16517. a, genitalia; b, penis interior; c, hermaphroditic duct; d, ovotestis; e, talon; f, pallial cavity. Scale lines as marked.

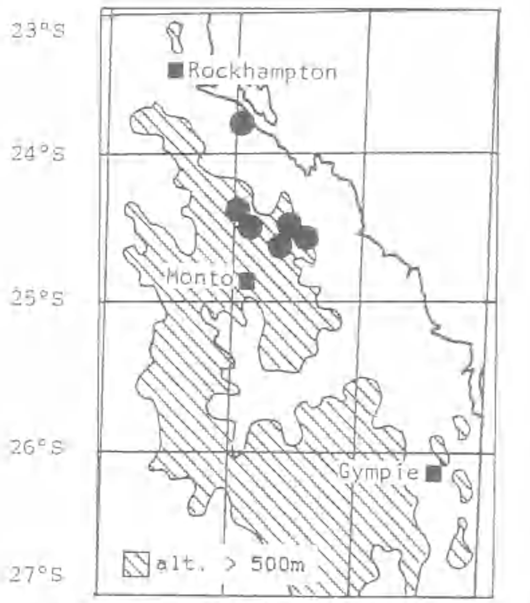


FIG 56. Distribution of *Gyrocochlea curtisiana* (Hedley, 1912).

of shell 2.52 mm, diameter 5.29 mm, H/D ratio 0.48, D/U ratio 3.45, whorls 4 1/4.

OTHER MATERIAL

Summit, Mt Booroon Booroon, SW of Miriam Vale, SEQ, MVF/*Araucaria*, litter (4, QMMO16860, 17 Sept 1985, J. Stanisic, D. Potter); Granite Creek, foothills of Bobby Range, SEQ (24°30.7'S, 151°30.3'E), under branch on ground (1, QMMO-14716, 7 Dec 1983, T. Carless); c. 1.8 km E of Builyan railway station, on Builyan-Gladstone Rd, SEQ (24°32'S, 151°24'E) rainforest next to river bank, litter (12, QMMO10319, 15 Jul 1980, J. Stanisic, A. Green); Dawes Range, SEQ, MVF/Araucaria (24°28'S, 151°07'E (47, QMMO12642, QM-MO12667, AMC136771, AMC136796, 4 Sept 1982, QM/QM-ABRS); base, Mt Booroon Booroon, SW of Miriam Vale, SEQ, rainforest along creek, under logs (3, QMMO16863, QMMO16594, 17 Sept 1985, J. Stanisic, D. Potter); Kroombit Tops, c. 13 km W of "Chapmans" SEQ (24°25'S, 151°02'E) NVF (12, QMMO12223, QMMO12224, AMC136552, AMC-136551, 6 Sept 1982, AM/QM-ABRS); Mt Fort William, Kalpowar S.F., SEQ, NVF (2, QMMO12597, AMC136756, 4 Sept 1982, AM/QM-ABRS); c. 4 km below summit of Mt Fort William, Kalpowar S.F., SEQ, MVF/*Araucaria*, under logs and rocks (2, QMMO17011, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton); Mt Fort William, Kalpowar S.F., SEQ, CNVF, 833 m, under logs (2, QMMO16822, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton); Kroombit Tops, SEQ, open forest (3, QMMO16453, 30 Sept 1985, G.B. Monteith); Kroombit Tops, SEQ, MVF/NVF, under palm fronds and logs (30, QMMO-16517, 10 May 1984, J. Stanisic, D. Potter).

DIAGNOSIS

Shell large, diameter 4.71–5.97 mm (mean 5.38 mm) with 4 1/8 to 4 3/4 (mean 4 1/2-) tightly coiled whorls. Last whorl descending in front. Apex and early spire (Fig. 54a) almost flat, SP/BWW ratio 0.04–0.05 (mean 0.04), to depressed. Height of shell 2.52–3.28 mm (mean 2.84 mm), H/D ratio 0.47–0.65 (mean 0.53). Protoconch of 1 3/8 to 1 5/8 whorls, mean diameter 718.8 μm at 1 1/2 whorls. Apical sculpture (Figs 54e, 64a) of curved radial ridges crossed by very low spiral cords which are partially fused and worn, producing a pitted appearance. Post nuclear sculpture (Fig. 54f) of numerous, crowded, protractively sinuated radial ribs, 93–159 (mean 125.8) on the body whorl. Ribs/mm 6.13–9.12 (mean 7.42). Microsculpture (Fig. 54f) of fine thread-like radial riblets, 7–15 between each pair of major ribs and low crowded spiral cords which buttress the microradials on either side. Microspirals continuous on the major radials. Umbilicus (Fig. 54b) wide, V-shaped, diameter 1.45–1.92 mm (mean 1.69 mm). D/U ratio 2.76–3.52 (mean 3.23). Sutures deeply impressed. Whorls rounded below and shouldered above a weakly rounded periphery (Fig. 54c). Aperture broad, ovately lunate. Lip simple. Parietal callus present. Colour variable, light-yellow horn with red chevron-like markings, to dark-brown. Based on 17 measured adults.

Epiphallus (Fig. 55a) long, muscular, entering penis subapically. Upper portion of epiphallus connected to penial sheath (Fig. 55a) by long fibres. Penis (Fig. 55b) long, muscular, internally with several longitudinal pilasters, more slender and more crowded apically. Epiphallus entering through a pore (Fig. 55b) surrounded by a spongy thickening. Penial retractor muscle (Fig. 55a) long, twisted around the epiphallus, inserted on the penis. Vagina long, internally with fleshy longitudinal pilasters.

Radula without unusual features.

Based on two dissected specimens (QMMO-16517).

RANGE AND HABITAT

G. curtisiana is confined to the Burnett-Cal-

TABLE 13. LOCAL VARIATION IN *BIOMPHALOPA RECAVA* (HEDLEY, 1912) AND *BIOMPHALOPA CONCINNA* (HEDLEY, 1924) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Biomphalopa recava Finch Hatton AMC 32992 (Holotype)	1	5 3/8	2.68	4.60	0.58		1.87		101	7.47	1.92	2.40
Eungella AMC 140230	1	5+	2.13	4.17	0.51	[illegible]	1.66	[illegible]	81	6.17	1.87	2.23
QMMO 11757	1	5 1/4-	2.47	4.69	0.53		1.83		94	6.38	2.00	2.34
Biomphalopa concinna Cardwell AMC 8902 (Holotype)	1	4 1/8	1.58	2.64	0.60		1.10	[illegible]	80	9.63	1.03	2.57
Kennedy S.F. QMMO 6417	1	4 7/8	1.87	3.45	0.54		1.49		95	8.76	1.23	2.80
Mt Bellenden Ker QMMO 11341	1	4 5/8+	1.61	2.81	0.58	[illegible]	1.28	[illegible]	80	9.05	1.23	2.28
QMMO 14877	1	5 1/8	1.79	3.41	0.53	[illegible]	1.53	[illegible]	84	7.84	1.27	2.68

liope-Many Peaks-Dawes Ranges, SEQ, with an outlier population at Mt Larcom. As with other *Gyrocochlea*, *G. curtisiana* occurs outside of larger rainforest areas and has been collected in remnant rainforest at Builyan, SEQ, and 'open forest' at Kroombit Tops. *G. curtisiana* favours warm subtropical notophyll vine forests but may be found in adjacent microphyll vine forest (with *Araucaria*).

REMARKS

The pitted apical sculpture, almost flat spire, rounded body whorls and flammulated shell of *G. curtisiana* (Fig. 54a,c,e) are departures from the average *Gyrocochlea* pattern. However genital anatomy, in particular the form and internal characteristics of the penis (Fig. 55b), is typical.

Biomphalopa gen. nov.

ETYMOLOGY

From the Greek omphalos, meaning umbilicus; referring to biconcave appearance.

TYPE SPECIES

Endodonta recava Hedley, 1912.

PREVIOUS STUDIES

Hedley (1924) introduced *Gyrocochlea* for charopids with biconcave shell and prominent radial sculpture on adult whorls, and included *G. concinna* Hedley, 1924 and *Endodonta recava* Hedley, 1912. These species, characterised by boldly ribbed, tightly coiled biconcave shells on which the protoconch is macroscopically smooth and glossy, are here separated to a new genus.

DIAGNOSIS

Shell diameter range 2.64–4.69 mm, with 4 1/8 to 5 3/8 tightly coiled whorls, last descending more rapidly. Apex and early spire deeply sunken. Apical sculpture of regularly arranged pits and vague radial ridges. Post nuclear sculpture of high, bold, crowded, protractively sinuated radial ribs. Microsculpture of fine radial riblets and equally fine spiral cords, continuous on the surface of the major radials. Umbilicus wide and cup-shaped. Sutures becoming deeply furrowed as the last whorl descends. Whorls strongly shouldered above and rounded below a laterally compressed periphery. Aperture acute ovately lunate. Colour creamy-white with darker radial suffusions.

Animal with long slender foot and varying degrees of black speckling on the visceral coil.

Kidney with pericardial lobe long and slender, rectal lobe reduced. Male genitalia with epiphallus shorter than penis, muscular, entering penis sub-apically through a simple pore. Penis without a sheath, either tubular with a large central longitudinal pilaster and a group of smaller apical longitudinal pilasters (*recava*), or with a swollen apical section containing a large corrugated verge (*concinna*). Terminal female genitalia with very long vagina and free oviduct. Radula with tricuspid central and laterals in which mesocone is long, slender lanceolate.

DISTRIBUTION AND ECOLOGY

Biomphalopa recava is found in subtropical notophyll vine forests of the foothills and uplands of the Eungella Range whereas *B. concinna* occurs mainly in notophyll vine forests of the Cardwell Range and montane vine fern thickets and vine forests of the Bellenden Ker Range. Both species live under logs.

COMPARISONS

Biomphalopa is distinguished from *Gyrocochlea* by its smaller size (Table 11), greater number of tightly coiled whorls, bolder radial ribs and wider, cup-shaped umbilicus. *Nautiliropa* also has a sunken spire with pitted apical sculpture (Fig. 63d) but is larger, has fewer, loosely coiled whorls, finer and structurally different radial ribbing (Fig. 63e) and a body whorl which does not descend (Fig. 63c). Anatomically the terminal male genitalia of *Biomphalopa* bear some similarities to those of *Gyrocochlea* but the lack of a penis sheath and presence of a single longitudinal penial pilaster contrast with *Gyrocochlea* (Fig. 46b). The superficially similar *Nautiliropa* has a pear-shaped penis with quite complex pilasters (Fig. 65c). *Biomphalopa* can be readily derived from *Gyrocochlea* and common ancestry is probable.

Biomphalopa recava (Hedley, 1912)
comb. nov.
(Figs 57–59; Tables 11, 13)

Endodonta recava Hedley, 1912, p. 267, pl. 10, figs 58–60.

Gyrocochlea recava (Hedley); Hedley, 1924, p. 217; Iredale, 1937a, p. 323.

COMPARISONS

B. recava differs from *B. concinna* in its larger size, greater number of whorls, less crowded ribs and wider umbilicus. The penis of *B. recava* has a large central pilaster and group of smaller apical longitudinal thickenings in contrast to the slender central pilaster and large corrugated apical pilaster of *B. concinna*.

TYPE MATERIAL

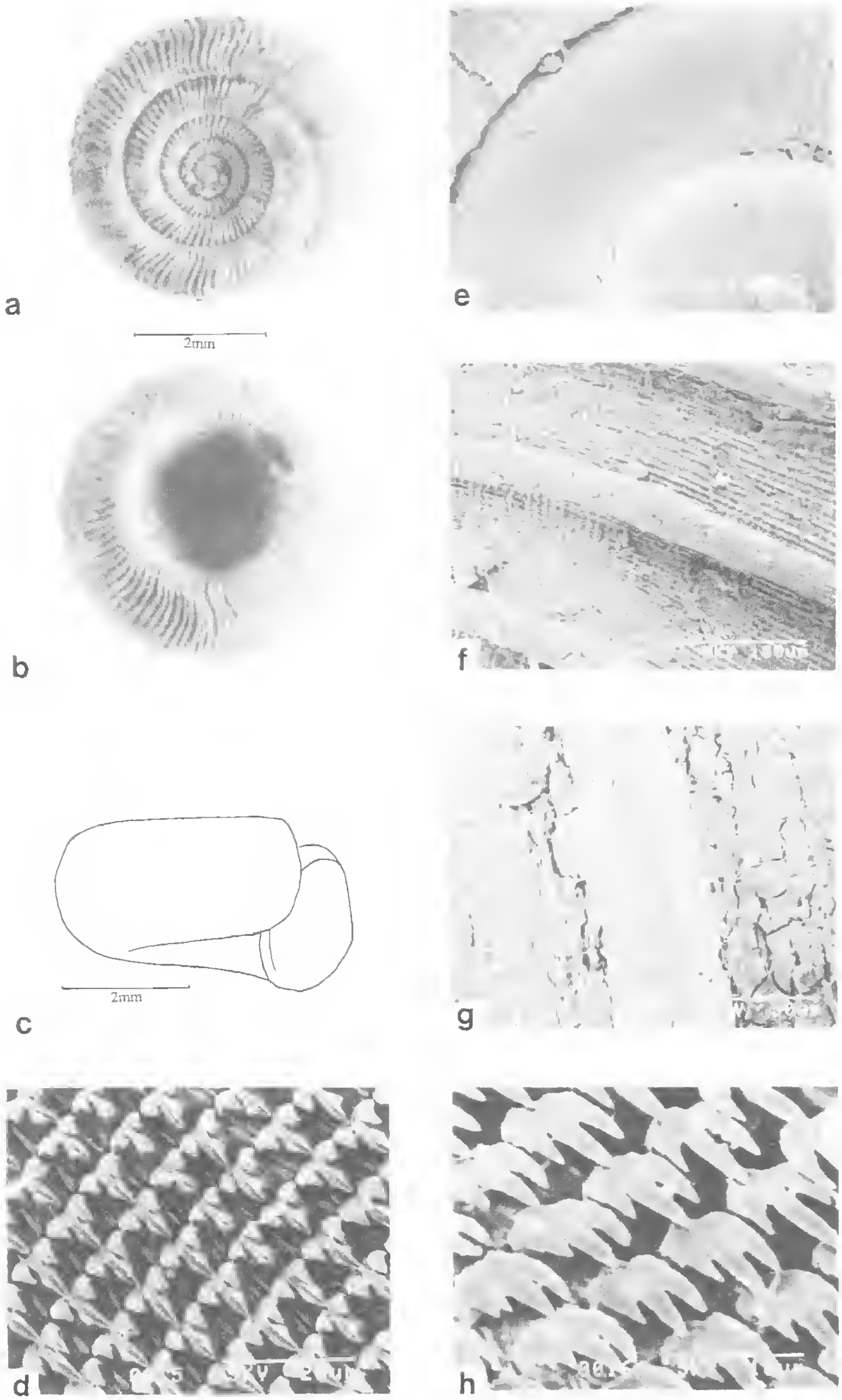
HOLOTYPE:: AMC32992, Finch Hatton, W of Mackay, MEQ. Scrub. Collected by S.W. Jackson, 2 Sept 1908. Height of shell 2.68 mm, diameter 4.60 mm, H/D ratio 0.58, D/U ratio 2.40, whorls 5 3/8.

OTHER MATERIAL

Eungella Range, 50 miles W of Mackay, MEQ (2, AMC140230, Sept 1957, L. Price); Finch Hatton N.P., W of Mackay, MEQ (21°04'S, 148°38'E), 180 m, (2, AMC153726, 29 Apr 1975, J.B. Burch, W.F. Ponder, P.H. Colman); Digging's Rd, Eungella N.P., MEQ (21°09'S, 148°29'E) NVF (10, QMMO11757, QMMO13073, 8 Jul 1982, J. Stanisic); Palm Walk, Eungella N.P., MEQ (21°00'S, 148°30'E) 800 m, CNVF (1, QMMO6345, Nov 1976, M.J. Bishop); Dalrymple Heights, Eungella N.P., MEQ, NVF, 1000 m (2, QMMO6367, Nov 1976, M.J. Bishop; 1, AMC153727, 28 Apr 1975, J.B. Burch, W.F. Ponder, P.H. Colman); Broken River, Eungella N.P., MEQ (21°10'S, 148°30'E) NVF (1, QMMO11715, 5 Jul 1982, J. Stanisic); Finch Hatton Gorge, c. 10 km N of Finch Hatton, MEQ (21°04'S, 148°38'E) NVF (1, QMMO11749, Jul 1982, J. Stanisic).

DIAGNOSIS

Shell diameter 4.17–4.69 mm (mean 4.49 mm) 5+ to 5 3/8 (mean 5 1/4-) very tightly coiled whorls, last descending very rapidly. Apex and early spire (Fig. 57a) deeply sunken, height 2.13–2.68 mm (mean 2.43 mm). H/D ratio 0.51–0.58 (mean 0.54). Apical sculpture (Fig. 57e) of pits and vague radial ridges. Protoconch of 1 5/8 to 1 3/4+ whorls, mean diameter 671.0 μm at 1 1/2 whorls. Postnuclear sculpture (Fig. 57f) of high, crowded, strongly protractively sinuated radial ribs, 81–100 (mean 91.7) ribs on the body whorl. Ribs/mm 6.17–7.47 (mean 6.67). Microsculpture (Fig. 57f) of fine radial riblets, 10–25 between each pair of major ribs and fine spiral cords which are continuous on the apices of the radial ribs. Umbilicus (Fig. 57b) very wide, cup-shaped, diameter 1.87–2.00 mm (mean 1.93 mm). D/U ratio 2.23–2.40 (mean 2.32). Sutures impressed becoming deeply furrowed as the last whorl descends. Whorls (Fig. 57c) shouldered above and below a laterally compressed periphery. Lip simple. Colour creamy-white with brown to reddish-brown radial flammula-


a
2mm
b
c
2mm
d
e
f
g
h

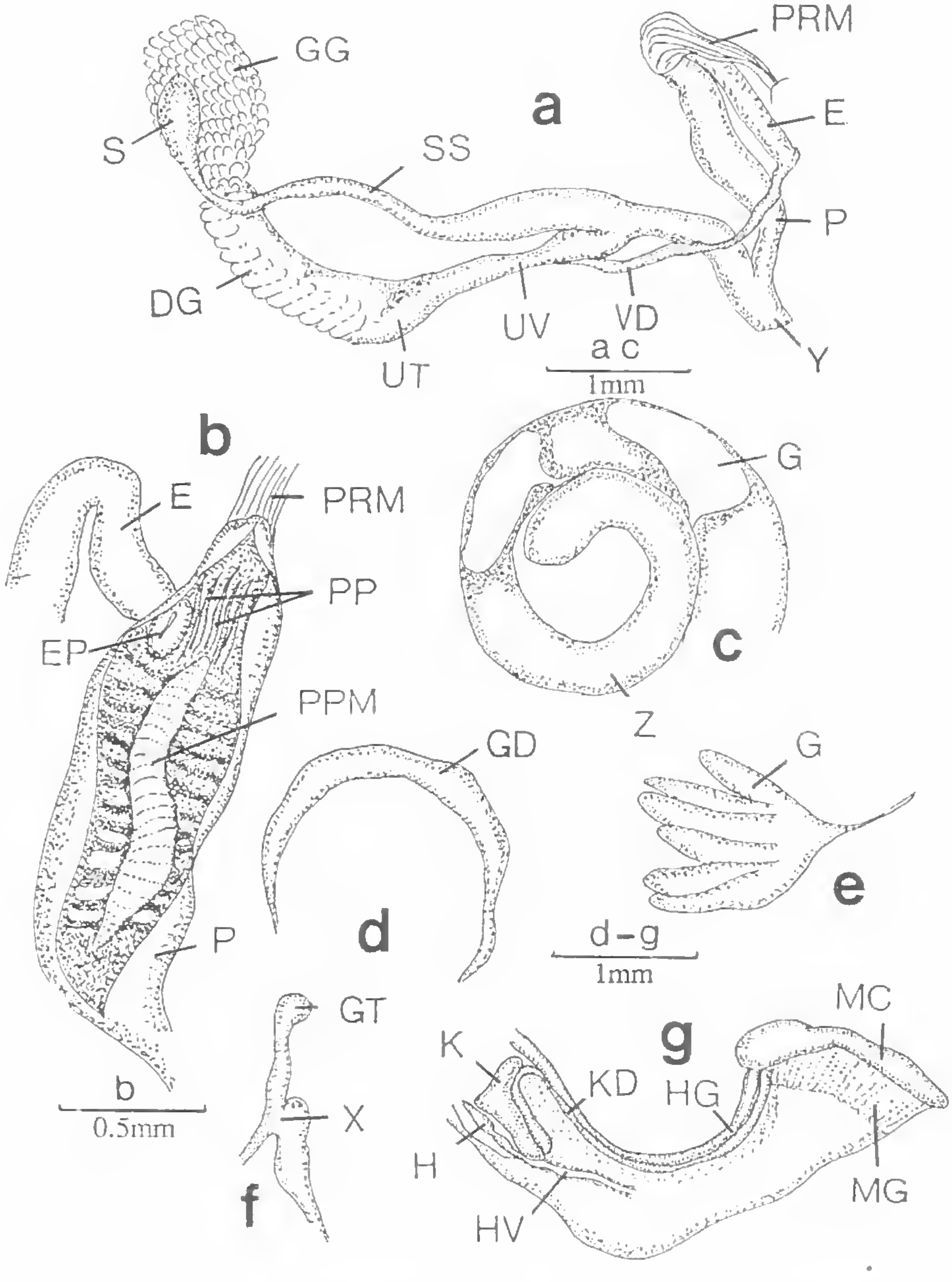


FIG. 58. *Biomphalopa recava* (Hedley, 1912). Digging's Rd, Eungella N.P., MEQ. QMMO11757. a, genitalia; b, penis interior; c, ovotestis; d, hermaphroditic duct; e, ovotestis; f, talon and carrefour; g, pallial cavity. Scale lines as marked.

FIG. 57. *Biomphalopa recava* (Hedley, 1912). a–c, Finch Hatton, W of Mackay, MEQ. AMC32992, holotype; d, h, Palm Walk, Eungella N.P., MEQ. QMMO6346; e–g, Digging's Rd, Eungella N.P., MEQ. QMMO11757. a–c, entire shell; d, central and lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, details of major radial rib; h, marginal teeth. Scale lines as marked.

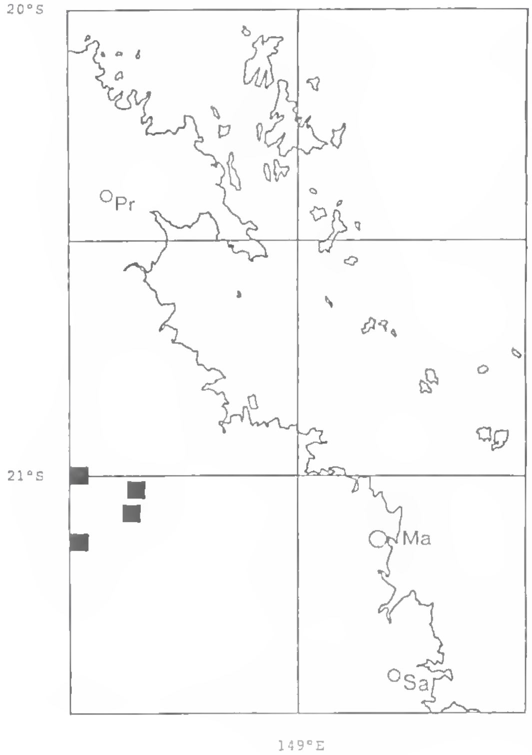


FIG. 59. Distribution of *Biomphalopa recava* (Hedley, 1912) in mid-east Queensland. (Pr = Proserpine; Ma = Mackay; Sa = Sarina).

tions. Parietal callus strongly developed. Based on 3 measured adults.

Genitalia with epiphallus (Fig. 58b) entering penis subapically through a simple pore (Fig. 58b). Penial retractor muscle inserting apically on penis head. Penis (Fig. 58b) swollen with a large central, longitudinal corrugated pilaster and shorter longitudinal pilasters apically. Free oviduct short, muscularised. Vagina long, internally with longitudinal pilasters.

Radula (Fig. 57d, h) typical.

Based on 4 dissected specimens (QMMO-11757, QMMO6345).

Range and Habitat

Under logs in warm subtropical notophyll vine forests of the Eungella area (southern extension of the Clarke Range) and Finch Hatton Gorge, MEQ. It has not been found in the drier rainforests of Mt Dryander, near Proserpine, MEQ.

Remarks

B. recava is distinguished by a biconcave shell with prominent radial ribs and tight coiling. *'Gyrocochlea' iuloidea* (Forbes, 1851), from Port Molle (=Airlie Beach), has a depressed spire and wide umbilicus but is larger with more loosely coiled whorls, apical sculpture of spirals and radials, broad V-shaped umbilicus, more rounded periphery, more prominent microspirals on the body whorl and monochrome, usually dark-brown, shell.

Biomphalopa concinna (Hedley, 1924) comb. nov. (Figs 60–62; Tables 11, 13)

Gyrocochlea concinna Hedley, 1924, p. 215, pl. 29, fig 1–3; Iredale, 1937a, p. 322.

Comparisons

See under *B. recava*.

Type Material

Holotype: AMC8902, Cardwell, NEQ. Height of shell 1.58 mm, diameter 2.64 mm, H/D ratio 0.60, D/U ratio 2.57, whorls 4 1/8.

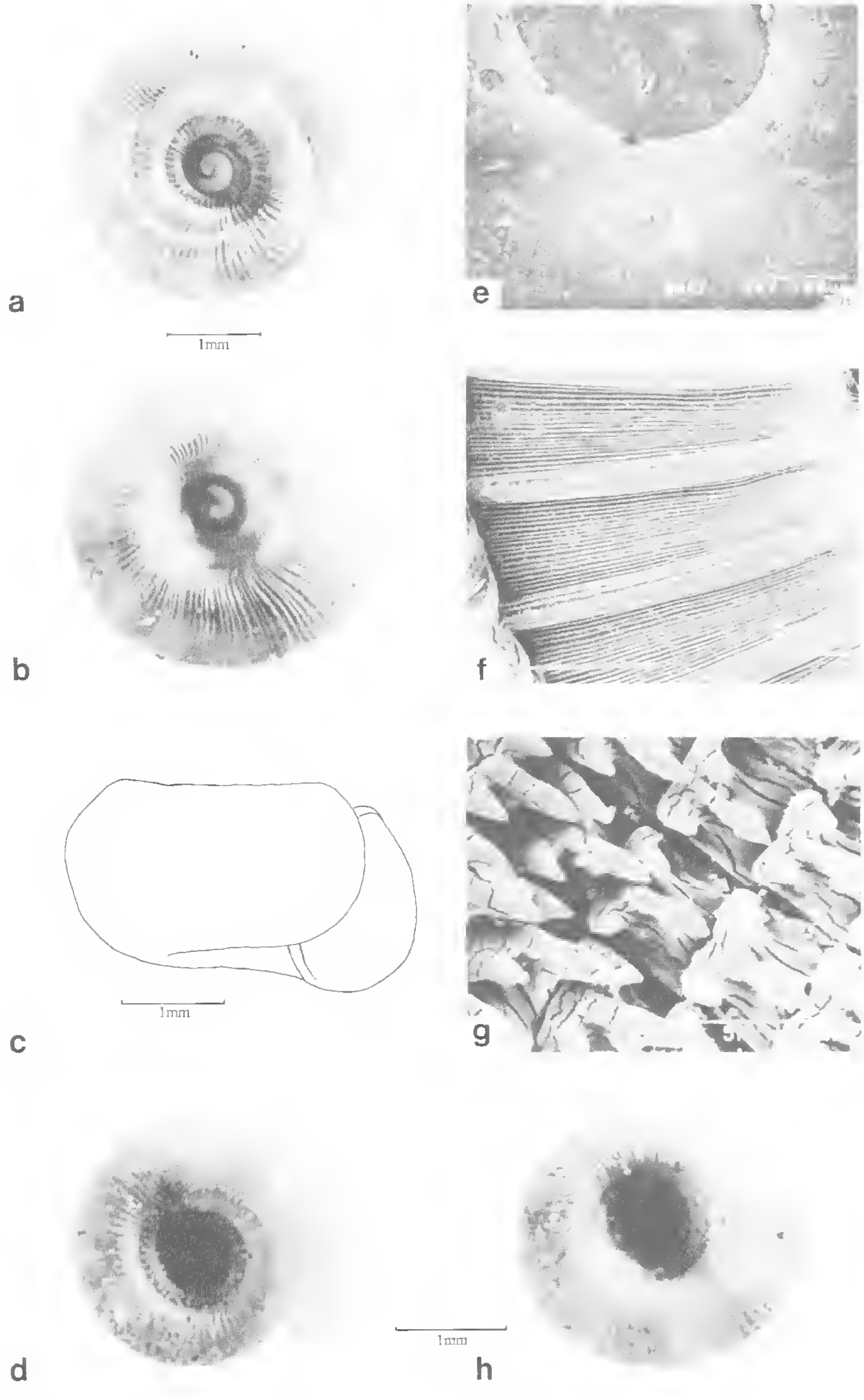
Other Material

Kirrama Range, via Kennedy, NEQ, 500 m, rainforest (1, QMMO17322, 2 Oct 1980, G.B. Monteith); Kennedy S.F., NEQ (18°13'S, 145°46'E), 900 m (1, QMMO6417, Aug 1977, M.J. Bishop); Dunn Creek, on Kirrama S.F. road, Cardwell Range, NEQ, NVF, (1, AMC142965, 27 Sept 1980, I. Loch); Mt Bellenden Ker, NEQ, just below summit, c. 1500 m, under bark on rotting log, MVFT (2, QMMO14878, 4 Jul 1983, J. Stanisic, D. Potter); Mt Bellenden Ker, NEQ (base, 17, QMMO11297; 500 m, 2, QMMO11326; 1054 m, 5, QMMO11343; summit, 5, QMMO11255; Earthwatch/QM, 1981); Mt Bartle Frere, NEQ, walking track below NW peak on western side, c. 1000 m, SNVF (2, QMMO11381, 8 Nov 1981, Earthwatch/-QM).

Diagnosis

Shell diameter 2.64–3.45 mm (mean 3.08 mm), 4 1/8 to 5 1/8 (mean 4 5/8+) tightly coiled

FIG. 60. *Biomphalopa concinna* (Hedley, 1924). a–c, Kennedy S.F., NEQ. QMMO6417; e–g, Mt Bellenden Ker, NEQ. QMMO14878, QMMO11297, QMMO11255; d, h, Cardwell, NEQ. AMC8902, holotype. a-c, d, h, entire shells; e, apicalsculpture; f, post nuclear sculpture; g, central and lateral teeth. Scale lines as marked.


a
1mm
b
c
1mm
d
1mm
e
f
g
h

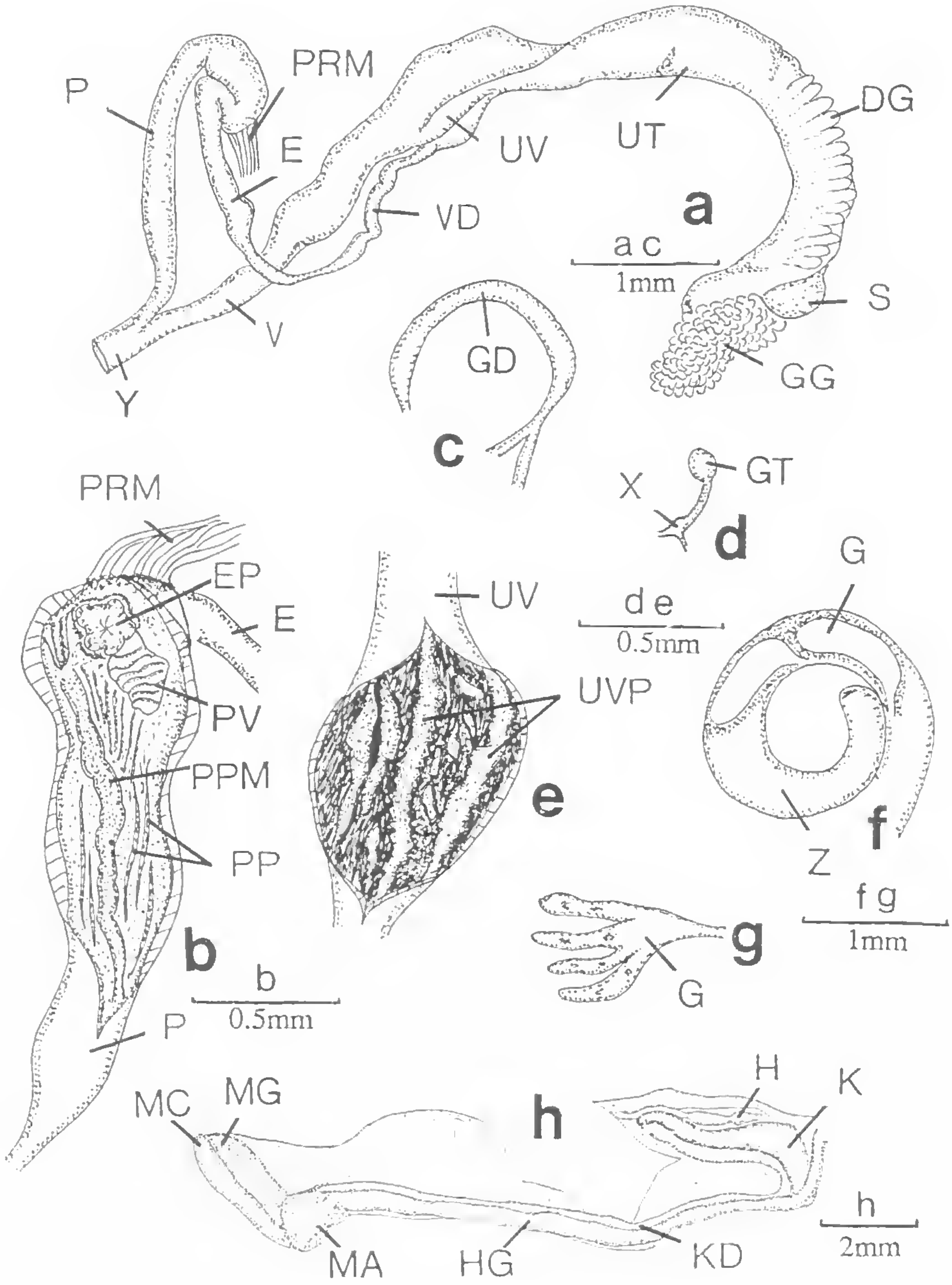


FIG. 61. *Biomphalopa concinna* (Hedley, 1924). Mt. Bellenden Ker, NEQ. QMMO11255. a, genitalia; b, penis interior; c, hermaphroditic duct; d, talon; e, interior of free oviduct; f, g, ovotestis; h, pallial cavity. Scale lines as marked.

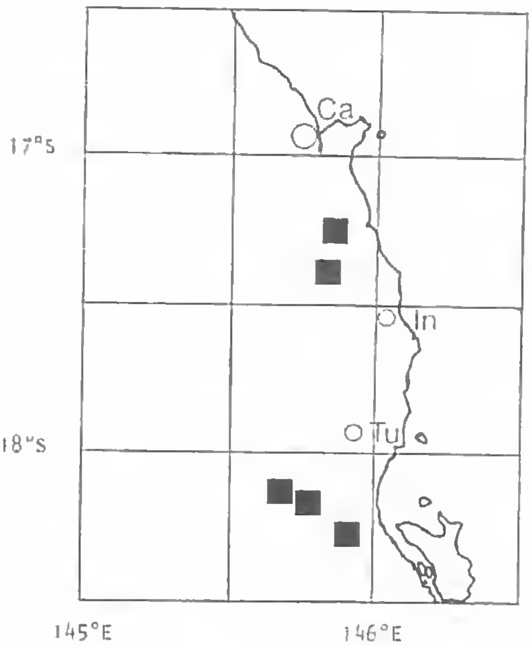


FIG. 62. Distribution of *Biomphalopa concinna* (Hedley, 1924) in north-east Queensland. (Ca = Cairns; In = Ingham; Tu = Tully).

whorls, last whorl descending more rapidly. Apex and early spire (Fig. 60a) strongly depressed, height 1.58–1.87 mm (mean 1.71 mm) H/D ratio 0.53–0.60 (mean 0.56). Protoconch glossy, 1 5/8 to 1 7/8 whorls, mean diameter 600.5 μm at 1 1/2 whorls. Apical sculpture (Fig. 60e) of radially arranged rows of pits. Post nuclear sculpture (Fig. 60f) of crowded, high, protractively sinuated radial ribs, 80–95 (mean 84.8) ribs on the body whorl. Ribs/mm 7.84–9.63 (mean 8.82). Microsculpture (Fig. 60f) of fine radial riblets, 6–20 between each pair of major ribs and fine crowded spiral cords, continuous on the apices of the radial ribs. Umbilicus very wide, cup-shaped, diameter 1.03–1.27 mm (mean 1.19 mm), D/U ratio 2.28–2.80 (mean 2.58). Sutures impressed, deep on the last whorl. Whorls rounded below and shouldered above a strongly compressed periphery (Fig. 60c). Lip simple, columella not expanded. Parietal callus strongly developed. Colour creamy-white to light-brown, with darker brown radial suffusions. Based on 4 measured adults.

Genitalia with large, muscular epiphallus which reflexes before entering the penis subapically (Fig. 61a). Penial retractor muscle inserted apically on the penis. Penis (Fig. 61b) with a large apical bulb, otherwise tubular, internally with an apical, fleshy swollen pilaster (Fig. 61b) adjacent to the simple epiphallic entrance. Penis proper with a single, thin, almost lamellate, longitudinal pilaster (Fig. 61b) and a few smaller thread-like longitudinal ridges, otherwise smooth. Free oviduct a short muscular tube. Vagina long, internally with very prominent corrugated longitudinal pilasters.

Radula (Fig. 60g) typical.

Based on two dissected specimens (QM-MO11255).

RANGE AND HABITAT

Under logs and under bark on rotting logs in the Kirrama Range, NE of Ingham, and the Bellenden Ker Range, SE of Cairns, NEQ; it prefers montane notophyll vine forests.

REMARKS

The verge in the penis indicates the possibility of sympatric relatives.

Nautiliropa gen. nov

ETYMOLOGY

Referring to the nautiloid-like appearance of the shell.

TYPE SPECIES

Helix omicron Pfeiffer, 1851.

DIAGNOSIS

Moderately large size, c. 4 1/2 tightly coiled whorls, the last inflated and not descending. Apex and early spire (Fig. 63a) strongly depressed. Apical sculpture of low radial ribs and low spiral cords, modified to produce a pattern of regularly arranged pits (Fig. 63d). Post nuclear sculpture (Fig. 63e) of numerous, protractively sinuated radial ribs formed by the periostracal extension of a single underlying radial thickening. Microsculpture of crowded microspirals and microradials. Umbilicus wide, U-shaped. Sutures impressed, whorls rounded below and shouldered above a rounded periphery (Fig. 64f). Aperture ovately lunate, lip simple.

Animal with long, slender foot, weakly speckled with darker pigmentation on the lower spire. Pallial cavity elongate with complete sigmurethrous ureter. Kidney with long pericardial lobe and vestigial rectal lobe. Epiphallus (Fig. 65b) not bound to the penial sheath, entering penis apically through a fleshy pilaster. Penis (Fig. 65c) pear-shaped with a muscular collar and a complex pilaster pattern. Penial bulb containing epiphallic entrance and horseshoe-shaped pilaster. Lower penial chamber with apical stimulator (Fig. 65c) and longitudinal thickenings. Terminal female genitalia short. Radula (Fig. 63c,f) with hook-like tricuspid central, bicuspid claw-like laterals without ectocone, and bicuspid marginals with long basal shafts and short endo- and ectocones. Teeth rows in a V-shape.

COMPARISONS

Nautiliropa omicron is removed from *Gyrocochlea* because of basic differences in major rib structure and coiling pattern. *Gyrocochlea* has major ribs composed of several small ribs, and a final whorl which descends (Fig. 45c), whereas *Nautiliropa* has a last whorl which coils more tightly without descending, and major ribs composed of a single rib with a large periostracal blade (Fig. 63e). Although the modified apical sculpture of *Nautiliropa* is also present in *Gyrocochlea curtisiana* (Hedley, 1912) this feature has evolved independently in several lineages of Charopidae.

Nautiliropa omicron (Pfeiffer, 1851)
comb. nov.
(Figs 63, 64d–f, 65, 66; Tables 11, 14)

Helix omicron Pfeiffer, 1851, p. 128; 1854, p.457, pl. 155, figs 13-17; Cox, 1868 p.18, pl. 10, fig.1.
Helix ammonitoides Reeve, 1854, pl. 181, sp. 1246.
Gyrocochlea omicron (Pfeiffer); Hedley, 1924, p. 216, pl. 30, figs 16–18; Iredale, 1937a, p. 323; Iredale, 1941a, p. 268.

COMPARISONS

N. omicron is most liable to be confused with species of *Gyrocochlea* which are sympatric with it in eastern parts of the McPherson Ranges, SEQ. The flammulated shell is good for field identification. However, rare monochrome brown specimens of *N. omicron* need to be distinguished by the more crowded radial ribs, smaller size, pitted apical sculpture and non-descending body whorl. *G. curtisiana* has a flammulated shell with crowded radial ribs (Fig. 54a) but lacks the strongly depressed spire of *N. omicron*.

PREVIOUS STUDIES

Early records of *Nautiliropa omicron* (Pfeiffer, 1851) cited by Cox (1868), Hedley and Musson (1892) and Hedley (1924), included records of *Gyrocochlea curtisiana* which is restricted to a small area from south of Miriam Vale to Mt Larcom, SEQ. Attempts to locate the type of *N. omicron* have been unsuccessful. Most probably it was housed in the Stettin Museum and destroyed during the World War II. The initial description and subsequent figures (Pfeiffer, 1854) leave no doubts as to the identity of the species.

TYPE MATERIAL

NEOTYPE: QMMO27290 (ex QMMO10501) Mt Warning N.P., NSW (28°24'S, 153°17'E), top of road in rainforest. Height 3.03 mm, diameter 5.71 mm, H/D ratio 0.53, D/U ratio 3.98, whorls 4 3/8-.

OTHER MATERIAL

W side of Somerset Dam, NW of Brisbane, NE of Esk, SEQ, open sclerophyll on hillside (2, AMC53175, 6 Sept 1970, W.F. Ponder & P. Marsh); NW of Brisbane, SEQ, Laceys Ck just S of Raynbird Ck., open dry sclerophyll and *Lantana* along creek, (27°14'S, 152°43'E) (2, AMC137792, QMMO12976, 30 Aug 1982, AM/QM-ABRS); c. 15 km from Legume on Acacia Plateau Rd., Koreelah Ck S.F., NE NSW, 800 m, NVF/MVF (10, AMC136824, QMMO12721, 8 Dec 1981, AM/QM - ABRS); Cooloola Nat. Park, SEQ (25°57'S, 153°06'E) SNVF on sand (7, AMC136487, AMC136490, QMMO12111, QMMO12113, 6 Sept 1982, AM/QM - ABRS); Coolomong Sanctuary, upper Currumbin Valley W of Tweed Hds, SEQ, rainforest reserve, litter (1, AMC137778, 30 Aug 1982, AM/QM - ABRS); Macpherson Ra., SEQ (1, AMC139778, Lower, ex Cox); Mt Tamborine, SEQ (2, AMC63795, J. Simmonds); Brisbane, SEQ (2, AMC139767, ex Cox); off trib. to Back Ck., Unumgar S.F., NE NSW (28°26'S, 152°42'E) (1, AMC128584, 15 Mar 1981, AM/QM - ABRS); Mt Nebo, W of Brisbane, SEQ (1, AMC140436, 23 Mar 1943, G.P. Whitley); Natural Bridge N.P., SEQ, NVF (28°13'S, 153°14'E) (8, AMC129269, AMC129271, QMMO10457, QMMO10460, 18 Mar 1981, AM/QM - ABRS); Mt Tamborine, SEQ, (1, AMC140439, J.A. Simmonds); Nth Pine River, SEQ, in scrubs (10, AMC103605, ex Cox); Little Yabba Ck., Imbil S.F., SEQ, NVF (26°28'S, 152°38'E) (2, AMC136448, QMMO12041, 7 Sept 1982, AM/QM - ABRS); sidetrack off Mt Archer Rd., Mt Mee S.F., SEQ.

NVF/*Araucaria* (27°04'S, 152°41'E) (8, AMC136523, QMMO12181, 31 Sept 1982, AM/QM - ABRS); Dandabah, Bunya Mts N.P., SEQ, behind picnic area (26°53'S, 151°36'E) (83, AMC136607, QMMO12283, 31 Sept 1982, AM/QM - ABRS); Murwillumbah, NSW (2, AMC139765, Lower, ex Cox); Mt Lindesay, Upper Richmond R., NSW (2,

TABLE 14 - LOCAL VARIATION IN *NAUTILIROPA OMICRON* (PFEIFFER, 1851) AND *LETOMOLA CONTORTUS* (HEDLEY, 1924) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Nautiliropa omicron												
Mt Warning QMMO 10501	3	4 1/4 (4 1/8–4 3/8-)	2.83±0.103 (2.69–3.03)	5.21±0.256 (4.87–5.71)	0.54±0.007 (0.53–0.55)	---	2.24±0.053 (2.19–2.35)	---	89.7±6.33 (77–96)	5.47±0.304 (5.02–6.05)	1.41±0.018 (1.38–1.44)	3.71±0.137 (3.54–3.98)
Natural Bridge N.P. OMMO 10457	1	4 1/2-	2.77	5.13	0.54	---	2.19	---	125	7.75	1.40	3.67
Binna Burra QMMO 16738	1	4 1/4	2.61	4.62	0.56	---	2.02	---	118	8.12	1.27	3.63
O'Reillys QMMO 16876	1	4 3/8	2.61	4.71	0.55	---	2.02	---	112	7.57	1.40	3.37
Mt Glorious QMMO 16127	3	4 3/8+ (4 1/4–4 5/8)	2.89±0.076 (2.77–3.03)	5.21 (4.87–5.46)	0.55±0.009 (0.54–0.57)	---	2.19±0.049 (2.10–2.27)	---	152.0±13.05 (126–167)	9.24±0.512 (8.22–9.79)	1.31±0.027 (1.27–1.36)	3.99±0.119 (3.91–4.22)
Mt Mee OMMO 7338	1	4 3/8	2.86	5.04	0.57	---	2.27	---	144	9.08	1.23	4.09
Blackbutt Range QMMO 12245	11	4 1/2+ (4 3/8–4 5/8+)	2.97±0.034 (2.77–3.11)	5.56±0.070 (5.21–5.97)	0.53±0.006 (3.30–3.86)	---	2.30±0.034 (2.10–2.52)	---	117.8±3.80 (89–131)	6.72±0.164 (5.43–7.29)	1.58±0.018 (1.46–1.64)	3.53±0.051 (3.30–3.86)
Cunningham's Gap QMMO 18534	1	4 3/8-	2.61	5.13	0.51	---	2.10	---	worn	---	1.54	3.33
Goomburra S.F. QMMO 12692	1	4 3/8+	2.35	4.37	0.54	---	1.93	---	72	5.24	1.31	3.33
Koreelah S.F. QMMO 10958	2	4 1/8- (4 -4 1/4-)	2.52±0.170 (2.35-2.69)	4.54±0.335 (4.20–4.87)	0.56±0.005 (0.55–0.56)	---	1.94±0.085 (1.85–2.02)	---	97	6.84±0.505 (6.33–7.34)	1.48±0.120 (1.36–1.60)	3.11±0.049 (2.62–3.60)
Bunya Mountains OMMO 12283	6	4 3/8- (4 1/8–4 1/2+)	2.79±0.045 (2.61–2.86)	5.32–0.046 (5.13–5.46)	0.52±0.011 (0.48–0.56)	---	2.06±0.029 (2.02–2.19)	---	104.5±3.91 (90–114)	6.25±0.249 (5.32–6.82)	1.50±0.041 (1.34–1.62)	3.57±0.102 (3.32–4.03)
Letomola contortus												
Sherwood AMC 28494 (Lectotype)	1	3 5/8-	0.80	1.81	0.44	---	0.64	---	---	---	0.64	2.84
Yessabah Caves AMC 119349	12	3 7/8- (3 1/2–4+)	0.92–0.016 (0.82–1.03)	2.07±0.035 (1.85–2.24)	0.45±0.01 (0.40–0.51)	---	0.69±0.008 (0.64–0.76)	---	---	---	0.78–0.018 (0.66–0.86)	2.67±0.05 (2.42–3.03)

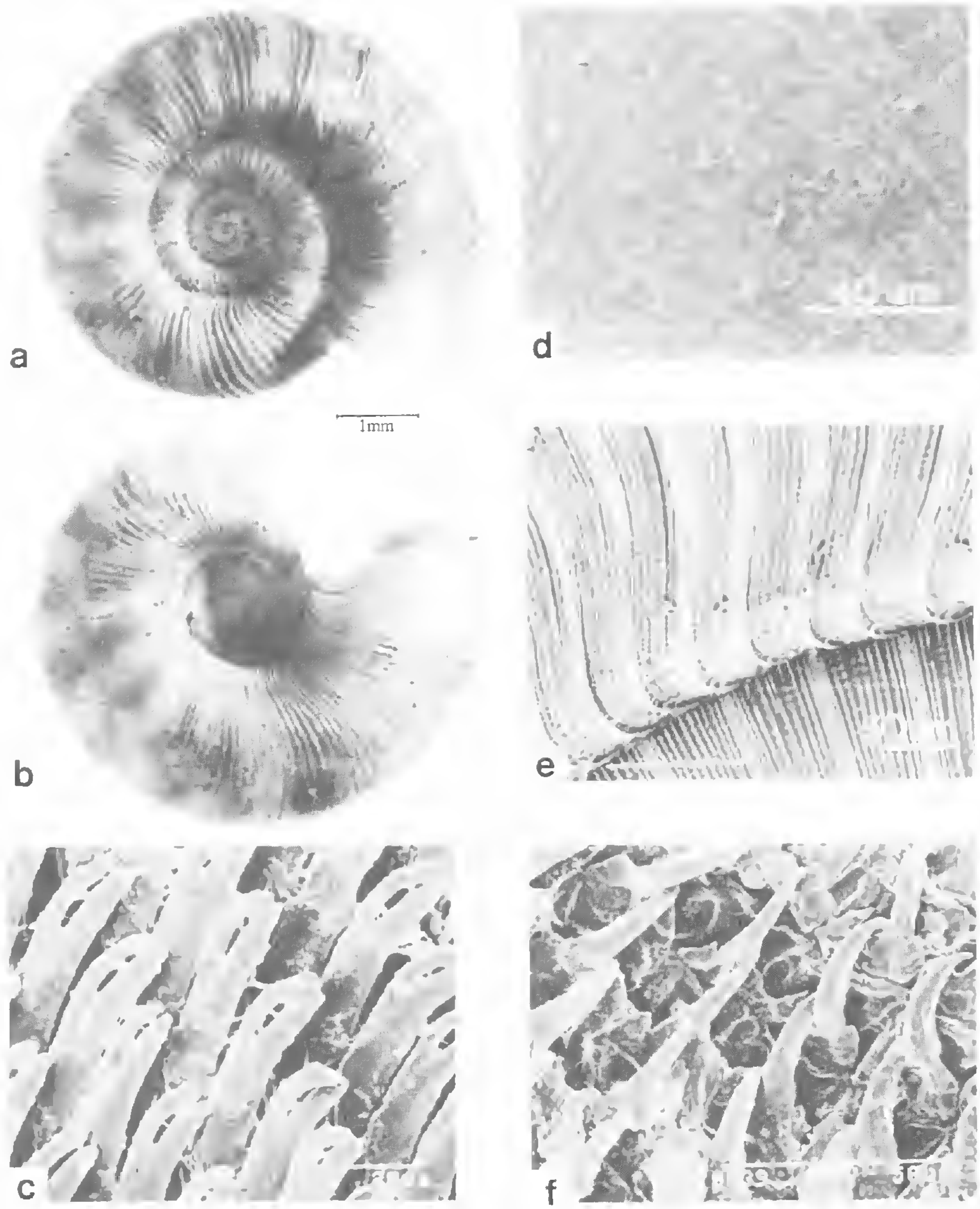


FIG. 63. *Nautiliropa omicron* (Pfeiffer, 1851). a–b, Mt Warning N.P., NSW. QMMO27290, neotype; c, f, Mt Glorious, SEQ. QMMO16127; d–e, Kenilworth S.F., SEQ. QMMO9688. a–b, entire shell; c, marginal teeth; d, apical sculpture; e, post nuclear sculpture; f, central and lateral teeth. Scale lines as marked.

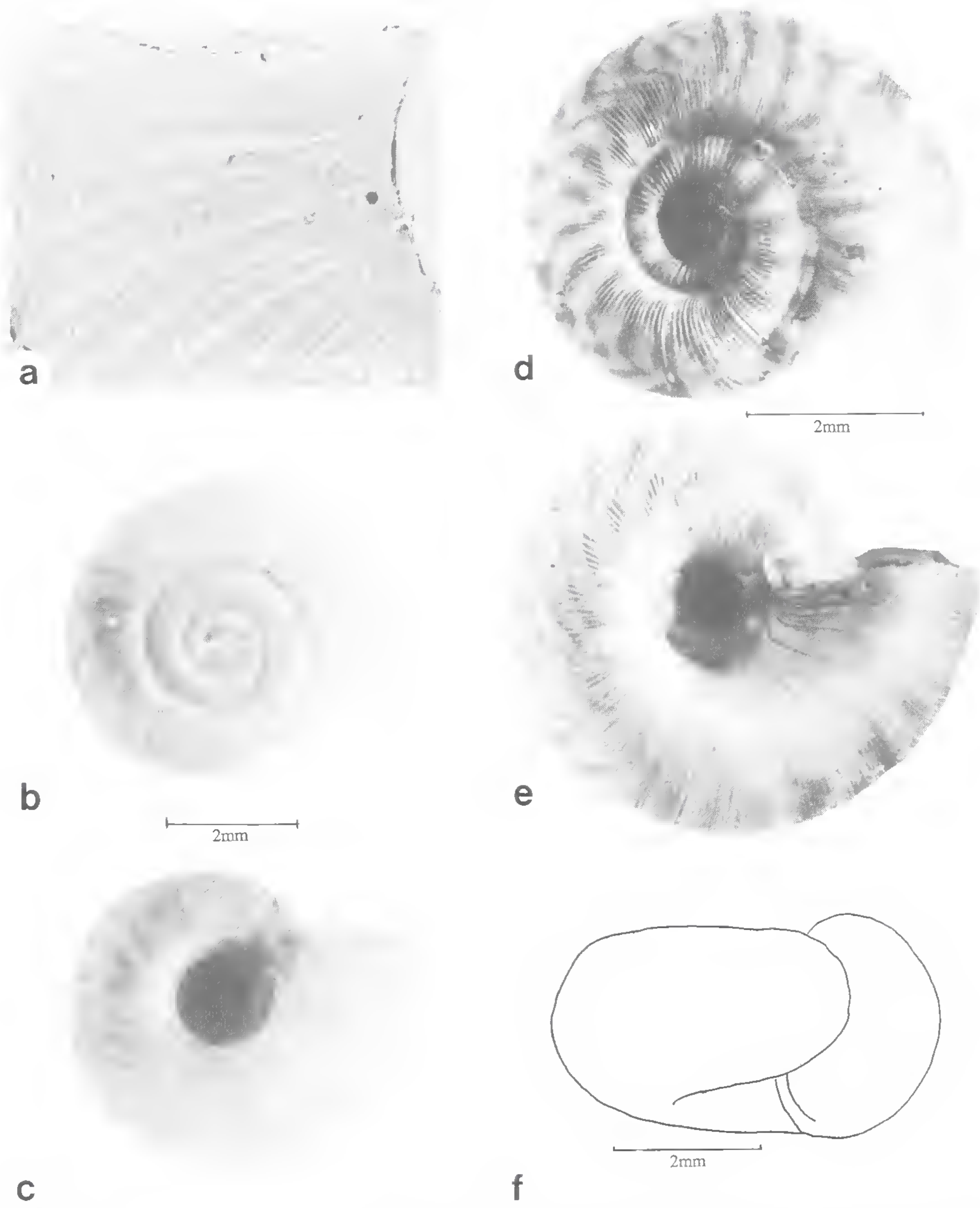


FIG. 64. a–c, *Gyrocochlea curtisiana* (Hedley, 1912). a, Kroombit Tops, SEQ. QMMO16453; b–c, Springs Scurb, Mt Larcom, SEQ. AMC32990, holotype. a, terminal part of protoconch; b, c, entire shell. d–f, *Nautiliropa omicron* (Pfeiffer, 1851). d-e, Mt Glorious, SEQ. QMMO16127; f, Dandabah, Bunya Mts, SEQ, QMMO12283. d–f, entire shell. Scale lines as marked.

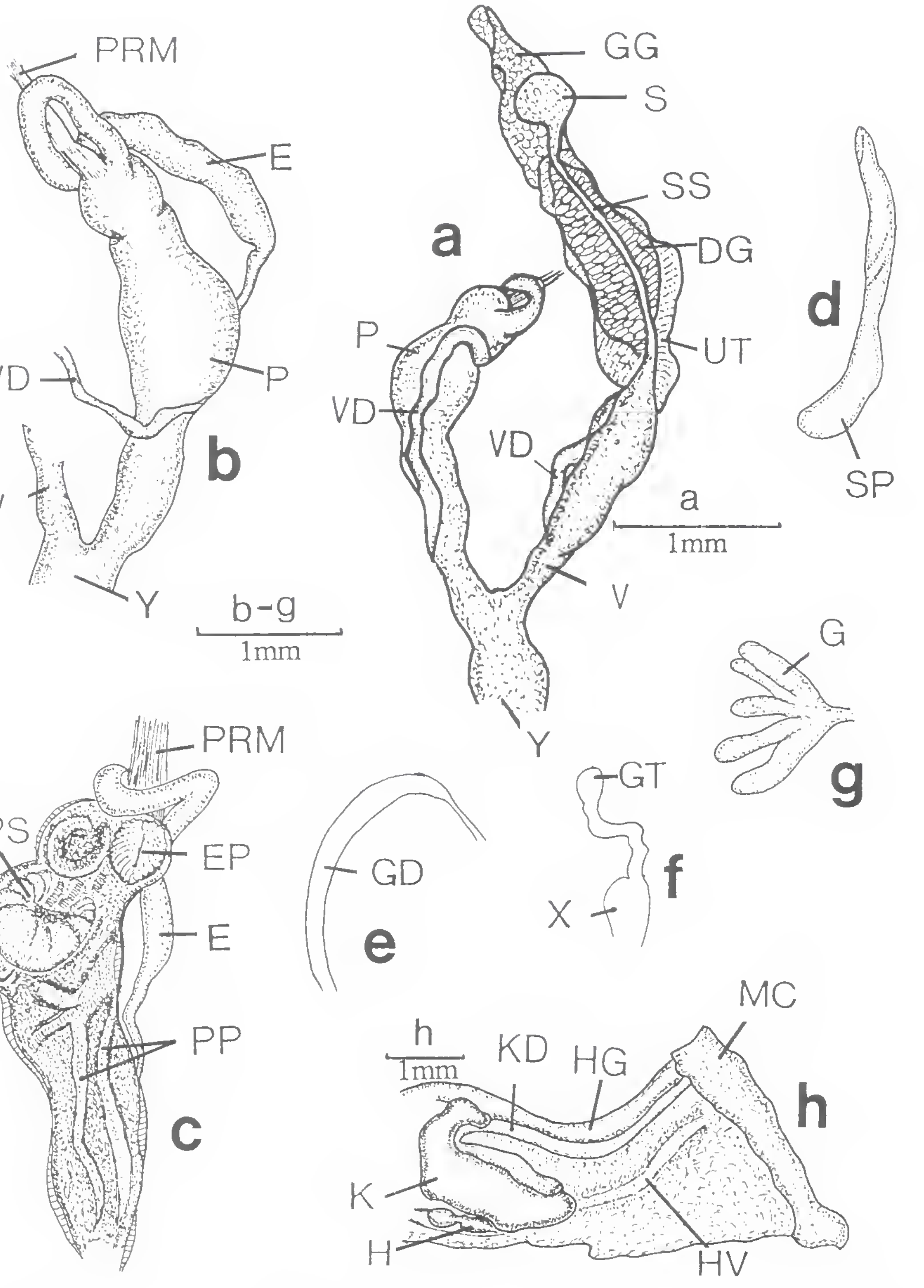


FIG. 65. *Nautiliropa omicron* (Pfeiffer, 1851). a–g, h, Mt. Glorious, SEQ. QMMO16127. f, Dandabah, Bunya Mts, SEQ. QMMO12283. a, genitalia; b, details of penial complex; c, penis interior; d, spermatophore; e, hermaphroditic duct; f, talon and carrefour; g, ovotestis; h, pallial cavity. Scale lines as marked.

AMC139761, 27 Apr 1958, L. Price); North Pine R., SEQ (2, AMC139762, Lower, ex Cox); Tweed R., NSW (6, AMC139768, Petterd, ex Cox); Canungra, SEQ (1, AMC32989, S.W. Jackson); Pine R., SEQ (2, AMC264, 1887, Musson); Goomburra S.F., Mistake Mts SEQ (27°59'S, 152°21'E) (6, AMC128619, QMMO11122, 16 Mar 1981, AM/QM - ABRS); c. 28.5 km from Goomburra, Goomburra S.F., SEQ 600 m, CNVF/Palms (27°59'S, 152°21'E) (17, AMC136814, QMMO12692, QMMO12698, 7 Dec 1981, AM/QM - ABRS).

Condamine R. Valley, c. 9 km NE of Killarney, NSW, along stream (28°18'S, 152°22'E) (3, AMC128907, QMMO10415, 16 Mar 1981, QM/QM - ABRS); Montville Rd, near Kondalilla Falls N.P. SEQ, vine scrub on roadside (26°40'S, 152°52'E) (5, AMC136414, QMMO11983, 8 Sept 1982, AM/QM - ABRS); Clarence R., NSW (3, AMC139758, ex Petterd); c. 3.5 km NW Mt Pleasant, on Dayboro - Mt Pleasant Rd., SEQ, dry and wet sclerophyll (27°08'S, 152°44'E) (4, AMC136497, QMMO12124, 30 Sept 1982, AM/QM - ABRS); c. 1 km S Raynbird Ck. Rd., on Laceys Ck. Rd., Laceys Ck., SEQ, open forest (27°14'S, 152°43'E) (10, AMC136476, QMMO-12090; AMC136482, QMMO12100, 30 Sept 1982, AM/QM - ABRS); Benarkin S.F., near Blackbutt, SEQ (8, AMC139757, Feb 1961, D.F. McMichael); Dandabah, Bunya Mts N.P., SEQ, behind picnic area (26°53'S, 151°36'E) (4, AMC136606, QMMO12282, 31 Sept 1982, AM/QM - ABRS); Clarence R., NSW (6, AMC139766, ex Cox); Tooloom Scrub, Beaury S.F. c. 8.3 km from Woodenbong, Legume Rd., NSW, MVF (28°29'S, 152°24'E), (1, AMC128534, 15 Mar 1981, AM/QM - ABRS); Cunninghams Gap N.P., SEQ, near monument, MVF (28°04'S, 152°24'E) (6, AMC128608, QMMO10991, 16 Mar 1981, AM/QM - ABRS); SW of Gympie, SEQ, NE slopes of Mt. Moorooreerai, remnant thicket amongst hoop pine plantation (26°16'S, 152°33'E) (7, AMC138105, QMMO13354, QMMO13356, 7 Sept 1982, AM/QM - ABRS); S of Gympie, SEQ, entrance to S.F. of Yabba Ck Rd near Dwyer Ck., remnant vine thicket along gully (26°28'S, 152°38'E) (4, AMC138111, AMC138112, QMMO13367, QMMO13369, 7 Sept 1982, AM/QM - ABRS); Richmond R., NSW (1, AMC139764, 1900, S.W. Jackson); Mt Warning N.P., NSW, top of road in rainforest (28°24'S, 153°17'E) (7, AMC129304, QMMO10501, 19 Mar 1981, AM/QM - ABRS); Blackbutt Range, c. 7.4 km S of Benarkin, SEQ, MVF/*Araucaria* (26°53'S, 152°11'E) (67, AMC136564, AMC136571, QMMO12238, QMMO12245, 31 Sept 1981, AM/QM - ABRS); O'Reilly's, Lamington N.P., SEQ (28°14'S, 153°15'E) (6, QMMO10439, 17 Mar 1981, AM/QM - ABRS); Mt Warning N.P., NSW, near base of Mt (28°24'S, 153°16'E) (2, QMMO10486, Mar 1981, AM/QM - ABRS); Toonumbar Forest Rd., Toonumbar S.F., c. 34 km from Kyogle NE NSW, CNVF (28°33'S, 152°45'E) (1, QMMO10912, 14 Mar 1981, AM/QM ABRS); Koreelah S.F., NE NSW, on Acacia Plateau Rd. c. 12.2 km from Acacia Ck - Killarney Rd., NSW, 850 m (28°21'S, 152°24'E), SEVT/MVF/*Araucaria* (3, QMMO10948, AMC128561, 15 Mar 1981, AM/QM - ABRS); Mt Glorious, c. 3 km SE of summit, SEQ (27°20'S, 152°46'E) (3, QMMO11991, QMMO11996, AMC136521, 2 Dec 1982, AM/QM - ABRS); Pomona S.F., SE of Pomona, SEQ (26°24'S, 152°54'E) (1, QMMO12006, 8 Sept 1982, AM/QM - ABRS 1982); Mt Guyra N.P., SEQ (25°49'S, 152°35'E) MVF/NVF/*Araucaria*, (2, QMMO12074, 7 Sept 1982, AM/QM - ABRS).

Byron Ck crossing, Byron S.F., c. 8.3 km NW of Mt Pleasant, SEQ (27°07'S, 152°43'E) (2, QMMO12159, AMC136500, 30 Sept 1982, AM/QM - ABRS); Cunningham's Gap N.P., SEQ, nr monument (28°04'S, 152°24'E) (13, QMMO12677, AMC136806, 7 Dec 1981, AM/QM - ABRS); Mt Warning N.P., NSW (28°24'S, 153°16'E), CNVF (1, QMMO12736, 15 Dec 1981, AM/QM - ABRS); S of Gympie, SEQ, entrance to Brooloo S.F. on Gibber Road, MVF (26°32'30"S, 152°41'30"E) (1, QMMO13377, 7 Sept 1982, AM/QM - ABRS); Upper Booloomba Ck, Conondale S.F., SEQ (26°41'S, 152°37'E) (1, QMMO13386, 8 Sept 1982, AM/QM - ABRS); Boombana N.P., Mt Nebo, SEQ, (1, QMMO6071, 14 Nov 1976, M.J. Bishop); Dandabah, Bunya Mts N.P., SEQ (27°53'S, 151°35'E) Araucaria/NVF, (20, QMMO6082, 5 Mar 1976, M.J. Bishop); Binna Burra, Lamington N.P., SEQ, 850 m, CNVF (2, QMMO6083, Apr 1976, M.J. Bishop); Manorina N.P., Mt Glorious, SEQ, wet sclerophyll (2, QMMO6263, Aug 1976, M.J. Bishop); Mt Byron S.F., SEQ (27°00'S, 152°30'E) (2, QMMO6277, Aug 1976, M.J. Bishop); Mt Glorious, SEQ (27°20'S, 152°46'E) (1, QMMO6293, Feb 1976, M.J. Bishop); Macdonald Park, Tamborine, SEQ, NVF (3, QMMO6306, 31 Aug 1976, M.J. Bishop); Boombana N.P., Mt Nebo, SEQ, wet sclerophyll (27°23'S, 152°47'E) (1, QMMO6344, Aug 1976, M.J. Bishop); Fred's Rd, Mt Mee SEQ, (27°05'S, 152°43'E) (11, QMMO7338, 14 Apr 1980, J. Stanisic, N. Hall, A. Green); Kenilworth S.F., SEQ (26°40'S, 152°36'E) *Araucaria*, (7, QMMO9688, 22 May 1980, J. Stanisic, A. Green); Maiala N.P., Mt Glorious, SEQ, CNVF (22, QMMO11604, QMMO11847, 20 Jun 1982, MSA party); Spicer's Gap, SEQ (1, QMMO11838, 7 Aug 1982, A. Rozefelds).

Mt Nebo, SEQ., nr Jolly's Lookout, NVF (1, QMMO12771, 2 Dec 1982, J. Stanisic); Kenilworth

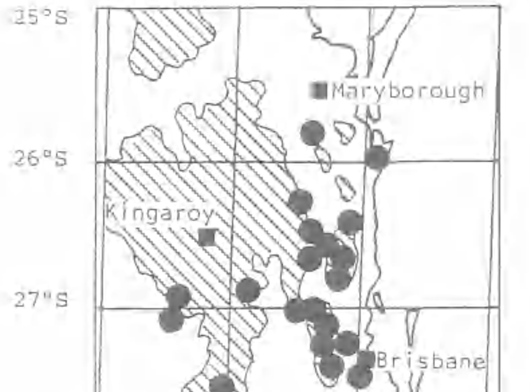


FIG. 66. Distribution of *Nautiliropa omicron* (Pfeiffer, 1851).

S.F., SEQ, c. 0.3 km N of Little Yabba Ck on Maleny to Kenilworth Rd, SEQ (26°37'S, 152°42'E) (3, QMMO13435, 19 May 1983, K. Collins, J. Stanisic); Mt Glorious, SEQ, NVF (6, QMMO14165, 28 Nov 1983, J. Stanisic); Boombana N.P., Mt Nebo, SEQ, NVF (1, QMMO15060, 5 Apr 1984, J. Stanisic); sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ (27°04'S, 152°41'E) (10, QMMO15074, 6 Sept 1983, J. Stanisic, D. Potter); Fred's Rd, Mt Mee, SEQ., NVF (27°05'S, 152°43'E) (2, QMMO15985, 28 Oct 1984, J. Stanisic, G. Annabell); Mt Glorious, SEQ., NVF (3, QMMO15989, 28 Oct 1984, J. Stanisic, G. Annabell); Mt Glorious, SEQ, NVF (11, QMMO16127, 26 Jan 1986, J. Stanisic, J. Chaseling).

Mt Tamborine, SEQ, Curtis Falls Circuit, CNVF, (1, QMMO16437, 23 Feb 1986, J. Stanisic, J. Chaseling); Upper Pine Ck., Canungra, SEQ, NVF/*Araucaria*, (1, QMMO16547, 1 Oct 1986, J. Stanisic, D. Potter); Redwood Park, Toowoomba, SEQ, NVF (7, QMMO16572, 10 Sept 1986, J. Stanisic); Araucaria Track, Binna Burra, Lamington N.P., SEQ, NVF (2, QMMO16578, QMMO16580, 27 Sept 1986, J. Stanisic); Tullawallal Circuit, Binna Burra, Lamington N.P., SEQ, NVF (7, QMMO16738, 2 Oct 1985, J. Stanisic, D. Potter, J. Chaseling); Natural Bridge N.P., SEQ, on roadside c. 300 m N of entrance, SNVF (5, QMMO16818, 29 Mar 1984, J. Stanisic); Blackbutt Range, SEQ., on side of Bruce Highway, MVF/*Araucaria* (51, QMMO16826, 12 May 1984, J. Stanisic, D. Potter); Mt Glorious, SEQ, CNVF (4, QMMO16832, 5 Apr 1984, J. Stanisic); Dandabah, Bunya Mts N.P., SEQ, NVF (14, QMMO16847, 12 May 1984, J. Stanisic, D. Potter); Big Falls Circuit, Bunya Mts N.P., SEQ, SNVF (19, QMMO16850, 5 Nov 1985, J. Stanisic, D. Potter); Cherry Plain - Westcott Plain Circuit, Bunya Mts N.P., SEQ, NVF/MVF (16, QMMO16856, 6 Nov 1985, J. Stanisic, D. Potter); Mt Hobwee Circuit, Binna Burra, Lamington N.P., SEQ, NVF (2, QMMO16865, 1 Oct 1985, J. Stanisic, D. Potter, J. Chaseling); Border Track, Binna Burra, Lamington N.P., SEQ, NVF (8, QMMO16870, 10 Mar 1984, J. Stanisic).

Tullawallal Circuit, nr antarctic beeches, Binna Burra, Lamington N.P., SEQ, NVF (1, QMMO16874, 11 Mar 1984, J. Stanisic); Border track, nr O'Reillys, Lamington N.P., SEQ, NVF (7, QMMO16876, 31 Mar 1984, J. Stanisic); initial part of Kweebani Caves Walk, Binna Burra, Lamington N.P., SEQ, NVF (4, QMMO16885, 9 Mar 1984, J. Stanisic); Kenilworth S.F., SEQ (26°37'S, 152°42'E) (1, QMMO18530, 22 May 1980, J. Stanisic, A. Green); Mudgeeraba, SEQ, (3, QMMO18531, C.J. Wild); Cunningham's Gap, SEQ, (4, QMMO18532, QMMO18534, 18 Jun 1979, G. Annabell); Mt Nebo, c. 2 km east of summit, SEQ, (152°47'E, 27°24'S), NVF/Araucaria, (1, QMMO18533, 13 Aug 1980, J. Stanisic); Koondai-1 Lookout, Bunya Mts N.P., SEQ (26°53'S, 151°33'E), (1, QMMO18535, 2 Mar 1976, M.J. Bishop); Mary Cairncross Reserve, Maleny, SEQ, (26°46'S, 152°51'E), (1, QMMO18549, 22 May 1980, J. Stanisic, A. Green); c. 1.6 km N of Numinbah valley turnoff on Burleigh to Springbrook Rd, SEQ, NVF with palms (1, QMMO18550, 17 Dec 1980, J. Stanisic).

DIAGNOSIS

Shell large, diameter 4.20–5.97 mm (mean 5.24 mm) with 4 to 4 5/8+ (mean 4 3/8+) tightly coiled whorls, the last very inflated and not descending in front (Fig. 64f). Apex and early spire (Figs 63a, 64d) strongly depressed, height 2.35-3.11 mm (mean 2.82 mm). H/D ratio 0.48–0.57 (mean 0.54). Protoconch of 1 3/8 to 1 5/8 whorls (mean 1 3/8+) with mean diameter 597.5 μm at 1 1/2 whorls. Apical sculpture (Fig. 63d) of low, curved radial ridges and low spiral cords which are partially fused and worn producing a strongly pitted appearance. Post nuclear sculpture (Fig. 63e) of numerous, crowded, thin, protractively sinuated radial ribs, 72-167 (mean 113.6) ribs on the body whorl. Ribs/mm 5.02–9.79 (mean 6.90). Ribs with a high periostracal blade, often lost in dead or slightly worn specimens. Microsculpture (Fig. 63e) strongly reticulate, with fine microradials, 6–15 between each pair of major ribs and lower, crowded spiral cords which buttress the microradials on either side. Umbilicus (Figs 63b, 64e) wide, U-shaped, diameter 1.23–1.64 mm (mean 1.47 mm), D/U ratio 2.62–4.22 (mean 3.58). Sutures impressed, whorls rounded below and shouldered above a rounded periphery (Fig. 64f). Last whorl coiled more tightly. Aperture ovately lunate only slightly inclined from the shell axis. Lip simple, columella not expanded but slightly deflected toward umbilicus. Parietal callus well developed. Colour light-horn to light-brown, often with darker radial flammulations arranged in a zig-zag pattern. Based on 31 measured adults.

Genitalia with epiphallus (Fig. 65b) muscularised, looped around the penial retractor muscle before entering penis apically. Epiphallic pore (Fig. 65c) between two swollen pilasters. Penis (Fig. 65c) pear-shaped with a distinct apical bulb, separated from the lower penial chamber by a constricting muscular collar. Penial bulb internally with apical to slightly lateral epiphallic entrance and horseshoe-shaped pilaster. Lower penial chamber with a large apical pocket stimulator (Fig. 65c), and anastomosing spongy thickenings.

Penial retractor muscle short, inserting on penis apex adjacent to epiphallus. Vagina long internally with fleshy longitudinal thickenings. Spermatophore, simple, clavate.

Radula as for genus.

Based on five dissected adults (QMMO16127, QMMO12283).

RANGE AND HABITAT

Highlands of the Great Dividing Range between Tooloom, NE NSW and the Bunya Mts, SEQ; the northern end of the Richmond Range; the McPherson Ranges south to the Tweed River, in the east; and the coastal and adjacent ranges north to Mt Guyra, SEQ. *N. omicron* shows preference for notophyll vine forests but also occurs in adjacent microphyll vine forests, wet sclerophyll forests, and in gallery rainforest along watercourses. *N. omicron* lives under logs.

REMARKS

N. omicron is one of the most conspicuous, widespread and frequently encountered of the subtropical microsnails. However most of the 637 specimens available were subadult reflecting the high proportion of mid-year, litter-collected material.

The modified radula of *N. omicron* is unparalleled in Australian charopids. Radulae of the large southern charopids *Mulathena fordei* (Brazier, 1871), *Stenacapha hamiltoni* (Cox, 1868) and *Thryasona diemenensis* (Cox, 1868) have typical central and lateral teeth (Smith and Kershaw, 1985) but marginals show modifications broadly similar to those in *N. omicron*. *M. fordei* and *S. hamiltoni* have strongly slanted, slender, unicuspid marginals while *T. diemenensis* has bicuspid marginals. In *N. omicron* the change from average charopid patterns may be the result of character displacement under conditions of microsympatry with the conchologically similar *Gyrocochlea*.

Specimens from eastern localities, in particular those from the D'Aguilar Range, SEQ, have more crowded ribs than those from the Great Dividing Range (Table 14). These differences may be related to local environmental conditions.

Letomola Iredale, 1941

Letomola Iredale, 1941a, p. 267.
Letomala (error) Kershaw, 1956b, p. 9.

TYPE SPECIES

Rhophodon contortus Hedley, 1924; by original designation.

PREVIOUS STUDIES

Iredale (1941a) introduced *Letomola* as monotypic. Smith and Kershaw (1979) included the Tasmanian species '*Helix*' *barrenensis* Petterd, 1879 without giving reasons and it is here excluded.

DIAGNOSIS

Small shell (mean diameter 2.05 mm), with few (mean 3 7/8-) tightly coiled whorls. Spire (Fig. 67a) depressed. Apical sculpture (Fig. 67d) of irregular malleations and ridgelets. Postnuclear sculpture of weak growth ridges and vague spiral cords. Umbilicus (Fig. 67b) very wide, cup-shaped (mean D/U ratio 2.68). Sutures impressed. Whorls rounded below the periphery, flattened at the basal margin with a strong supraperipheral sulcus above (Fig. 67c). Aperture ovately lunate with one parietal and one basal barrier (Fig. 68a, b). Lip simple, margins convergent. Colour brown with lighter streaks. Animal with foot and tail broad, bluntly rounded posteriorly. Live animal dark-grey, particularly on the sides of the foot above the pedal grooves, neck and mantle collar. Pallial cavity elongate with bilobed kidney, pericardial lobe reflexed. Genitalia with unusual features. Ovotestis a single, bilobed clump of follicles (Fig. 69c, d) embedded in the digestive gland. Terminal genitalia elongate. Epiphallus (Fig. 69a) a long slender tube, entering penis apically adjacent to an apical pilaster. Penis (Fig. 69b) slender with longitudinal pilasters. Penial retractor muscle inserted at the penis/epiphallus junction. Radula (Fig. 68d-f) narrow with few lateral and marginal teeth rows; central tooth very small, mesocone reduced; laterals tricuspid with much enlarged mesocone; marginals becoming multicuspid, serrate, with all cusps reduced in size.

COMPARISONS

L. contortus is conchologically distinctive with wide umbilicus (Fig. 67b), large, finely malleate protoconch (Fig. 67d), reduced adult sculpture (Fig. 67e, f), strong sulcus on the body whorl (Fig. 67c), and two apertural barriers (Fig. 68a, b). It is sympatric with *Rhophodon kempseyensis* (Fig. 77) which has a wide umbilicus and brown shell with white streaks but differs in having a radially lirate protoconch, extremely crowded ribs on the body whorl (mean ribs/mm 33.34), and more numerous apertural lamellae.

Letomola contortus (Hedley, 1924)
(Figs 67–70; Tables 11, 14)

Rhophodon contortus Hedley, 1924, p. 220, pl. 32, figs 35–37; Kershaw, 1955, p. 30.
Letomola contortus (Hedley); Iredale. 1941b, p. 2; Iredale, 1941a, fig. 6.
Letomala (sic) contortus (Hedley); Kershaw, 1956b, p. 9.

TYPE MATERIAL

LECTOTYPE: AMC28494, Sherwood, Macleay River NSW, ex Technological Museum (= collected by C. Laseron) Height of shell 0.80 mm, diameter 1.81 mm, H/D ratio 0.44, D/U ratio 2.84, whorls 3 5/8-.
PARALECTOTYPE: AMC150095, same data as lectotype.

OTHER MATERIAL

Yessabah Cave, W of Kempsey, NSW (31°06'S, 152°42'E), on roof and walls of limestone cave and in floor litter (200+, AMC119349, 9 Oct 1979, P.H. Colman, J. Stanisic); Yessabah Cave, via Kempsey, NSW (31°05'30"S, 152°41'E) vine thicket, on limestone rocks and in litter (54, QMMO17014, 3 Mar 1987, J. Stanisic, D. Potter, P.H. Colman).

DIAGNOSIS

Shell glossy, minute, diameter 1.81–2.24 mm (mean 2.05 mm) with 3 1/2 to 4+ (mean 3 7/8-) tightly coiled whorls. Apex and spire depressed with each whorl higher than the preceding whorl, except for the body whorl which descends in front. Height 0.80–1.03 (mean 0.91 mm). H/D ratio 0.40–0.51 (mean 0.45). Protoconch of 1 3/8 to 1 1/2- whorls, large, bulbous. Apical sculpture (Fig. 67d) of irregular malleations and ridges. Post nuclear sculpture (Fig. 67e) of broad radial ridges crossed by weak spiral cords, especially noticeable near the sutures. No additional microsculpture. Umbilicus (Fig. 67b) wide, shallow, cup-shaped, diameter 0.64–0.86 mm (mean 0.77 mm). D/U ratio 2.42–3.03 (mean 2.68). Sutures impressed, becoming a deep furrow as the last whorl descends. Whorls rounded below the periphery with a prominent supra-peripheral sulcus. (Fig. 67c). Aperture irregular ovately lunate with one parietal and one basal barrier. Basal barrier more deep-seated than parietal. Parietal barrier (Fig. 68a) extending 1/8 whorl, horizontal anteriorly, becoming angled downward posteriorly. Basal barrier (Fig. 68b) 1/8 whorl in length, following angle of coiling, tapered at either end. Lip simple, columella only slightly dilated, margins convergent. Parietal callus weakly developed. Colour deep reddish-brown with irregular white radial streaks, brown on the base. Based on 13 measured adults.

Epiphallus-vas deferens junction valvular. Epiphallus (Fig. 69b) entering penis apically. Penial retractor muscle inserted on the epiphallus-penis junction. Penis (Fig. 69b) a long tube with a slightly expanded apex. Epiphallic entrance a simple pore adjacent to a short tongue-like pilaster. Penis proper sculptured with longitudinal pilasters. Free oviduct and vagina long tubes without unusual features.

Radular characteristics as given in generic diagnosis.

Based on 6 dissected specimens (AMC-119349, QMMO17014).

RANGE AND HABITAT

From the limestone outcrop at Yessabah, west of Kempsey, NSW where the vegetation is semi-evergreen vine thicket. In spite of several collecting efforts it has not been found further westward in the limestones of the Carrai State Forest. *L.*

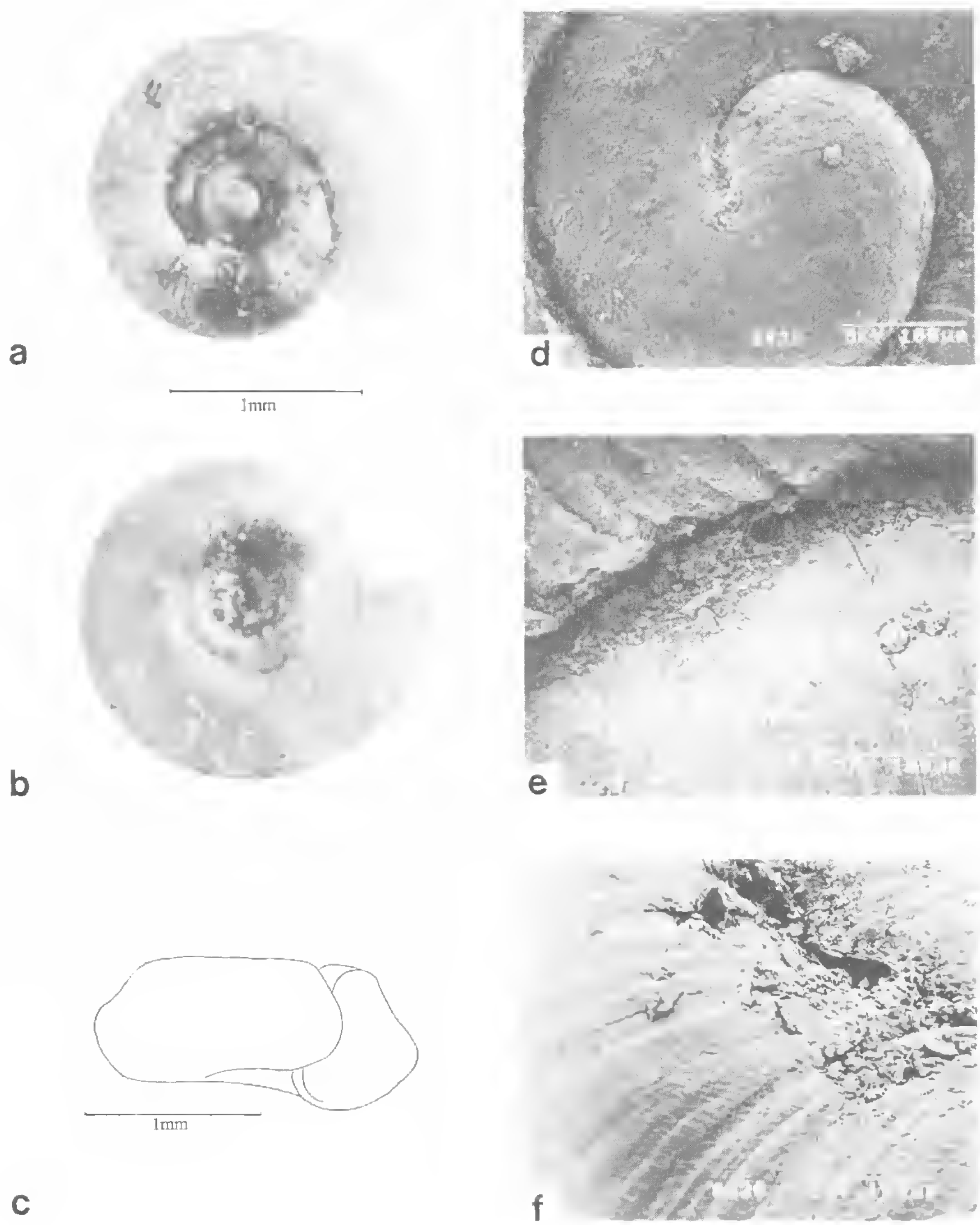


FIG. 67. *Letomola contortus* (Hedley, 1924). a–c, Sherwood, Macleay R, NSW. AMC119349. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, sculpture on base. Scale lines as marked.

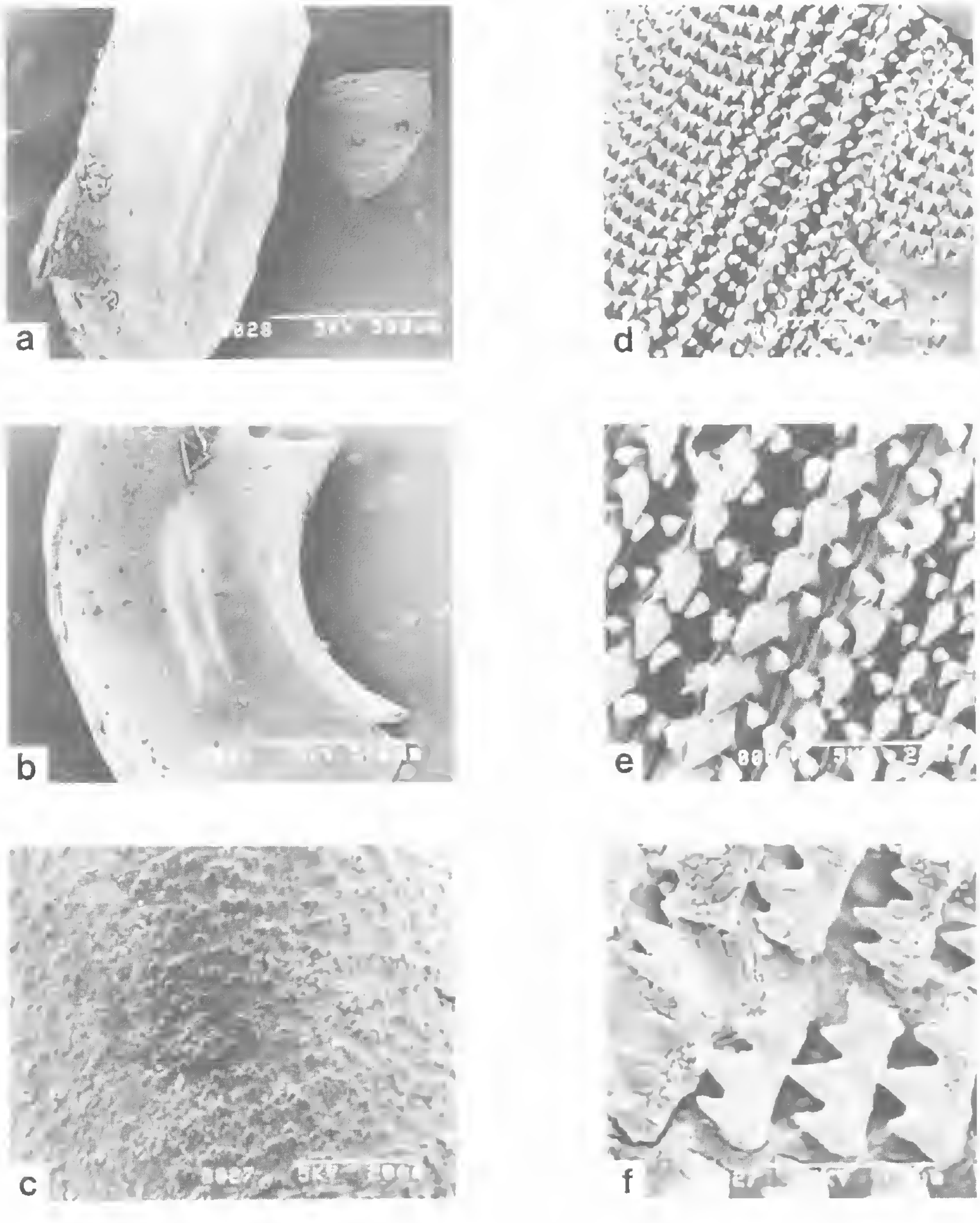


FIG. 68. *Letomola contortus* (Hedley, 1924). Yessabah Cave, W of Kempsey, NSW. AMC119349, QMMO17014. a, parietal barrier; b, basal barrier; c, microdenticulation on basal barrier; d, radula; e, central and lateral teeth; f, marginal teeth. Scale lines as marked.

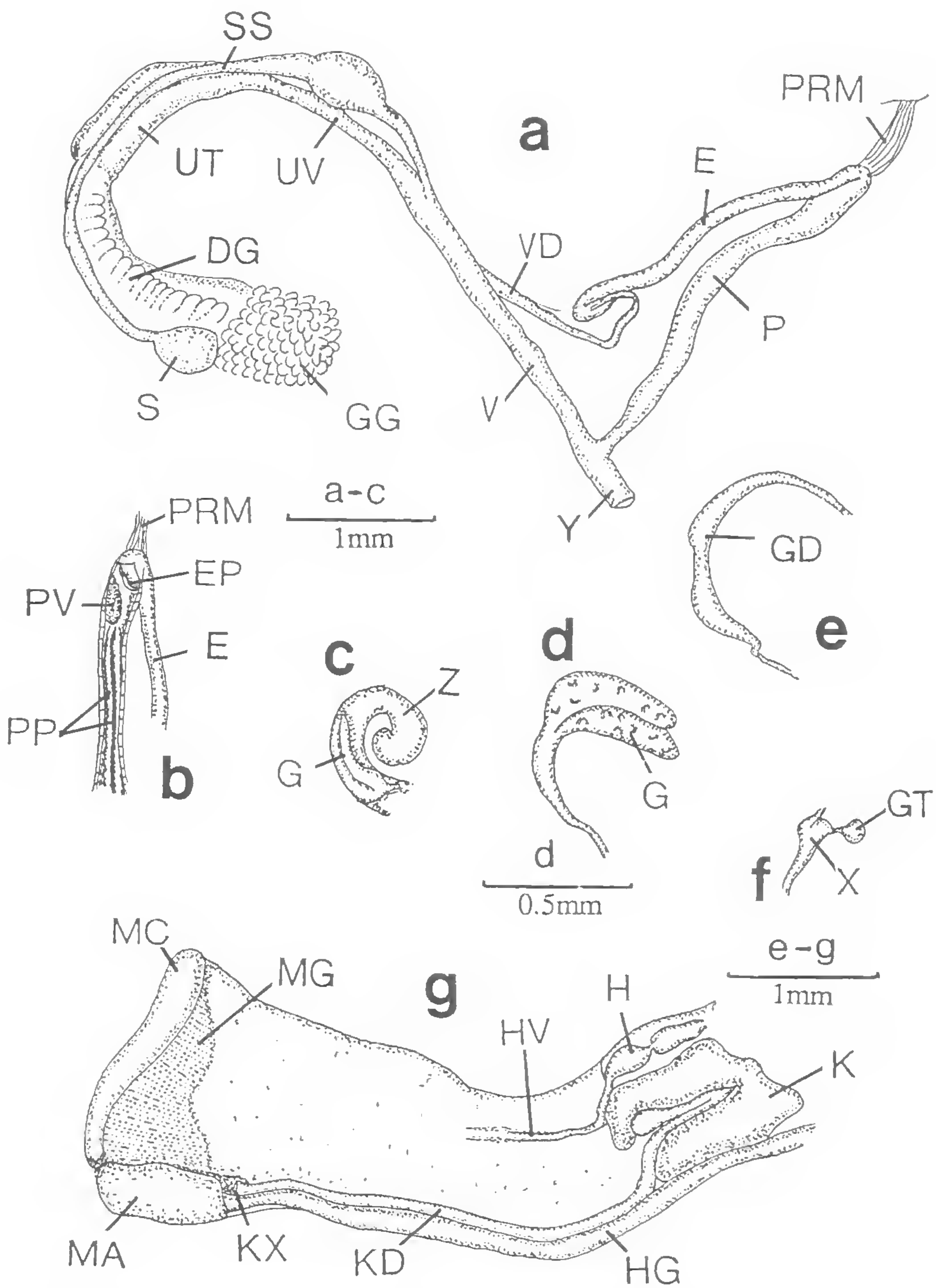


FIG. 69. *Letomola contortus* (Hedley, 1924). Yessabah Cave, W of Kempsey, NSW. AMC119349. a, genitalia; b, penis interior; c, d, details of ovotestis; e, hermaphroditic duct; f, talon and carrefour; g, pallial cavity. Scales lines as marked.

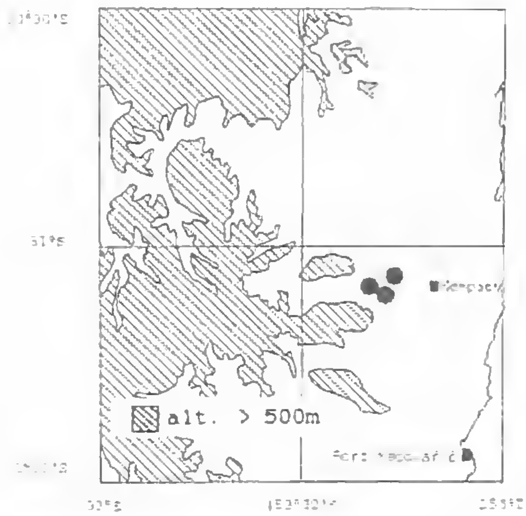


FIG. 70. Distribution of *Letomola contortus* (Hedley, 1924).

contortus has been collected live on limestone rocks after rain and presumably feeds on the microflora growing on the rock surface.

REMARKS

L. contortus displays a number of departures from typical charopid patterns. The malleated protoconch (Fig. 67d) and supraperipheral sulcus (Fig. 67e) are unusual features in the context of the east-coast species reviewed herein. Sulci are seen in some Pacific Island Endodontidae and Charopidae, and according to Solem (1983, p. 9) they are usually associated with keel formation. In *L. contortus* the sulcus indirectly constricts the size of the aperture. Anatomically the slender reproductive organs are more typical of the Punctidae. However, the radula is typically charopid even though the strong reduction in size of the central tooth and serrate appearance of the marginals are unusual. *Omphaloropa varicosa* has a grossly similar radula - few teeth per row and reduced central tooth.

Rhophodon Hedley, 1924

Rhophodon Hedley, 1924, p. 219; Iredale, 1937a, p. 329; Iredale, 1941b, p. 2; Kershaw, 1955, p.30; Burch, 1976, p.133.

Egilodonta Iredale, 1937a, p. 328; Kershaw, 1956a, p.142; Burch, 1976, p.132.

TYPE SPECIES

Rhophodon peregrinus Hedley, 1924; by original designation.

PREVIOUS STUDIES

Hedley (1924, p. 219) introduced *Rhophodon* for charopids with apertural barriers. Apertural barriers among Australian Charopidae are relatively rare but several generic groupings have been proposed including *Dentherona* Iredale, 1933 (type species: *Helix dispar* Brazier, 1871); *Bischoffena* Iredale, 1937 (type species: *Helix bischoffensis* Petterd, 1879); *Egilodonta* Iredale, 1937 (type species: *Charopa bairnsdalensis* Gabriel, 1930); and *Letomola* Iredale 1941 (type species: *Rhophodon contortus* Hedley, 1924). *Rhophodon* is expanded to include seven species of very small to minute charopids with apertural barriers and shells which have a predominantly radially lirate protoconch, post-nuclear sculpture of prominent radial ribs, and a wide saucer-shaped umbilicus.

DIAGNOSIS

Very small to minute Charopidae, diameter range 1.29–2.98 mm. Whorls 4 1/4 to 5 1/2-, tightly to very tightly coiled, last descending more rapidly. Apex and early spire depressed (*kempseyensis*, *peregrinus*) to very slightly elevated. Protoconch exsert of 1 1/2 to 1 3/4 whorls. Apical sculpture of numerous moderately crowded to very crowded (more so toward the protoconch - adult whorl boundary) weakly curved radial ribs and very weak thread-like spiral cords and cordlets. Post-nuclear sculpture of few, widely spaced (*colmani*, *bairnsdalensis*) to many, crowded (*kempseyensis*), thin, protractively sinuated to straight radial ribs. Microsculpture of numerous, crowded radial riblets, and widely spaced (*kempseyensis*) to crowded, low rounded spiral cords which are raised at their intersection with the radial riblets to form an elongate bead. Umbilicus wide, cup-shaped. Aperture ovately lunate, with few (*bairnsdalensis*) to many (*consobrinus*) barriers. Parietal barriers consisting of one to four (generally three) crescentic lamellae, with or without additional thread-like traces. Palatal barriers three to six (usually four) crescentic lamellae, with or without a superior trace. Columellar lamellae sometimes present. Pallial region elongate with almost unilobed kidney in which the pericardial lobe is well developed, reflexed at the tip, and the rectal lobe is reduced to a vestige abutting the hindgut.

Ovotestis two small clumps of finger-like lobes embedded in the subapical whorls of the digestive gland. Terminal male genitalia with epiphallus entering the penis apically or subapically (*consobrinus*) through two fleshy lips surrounded by a muscular collar. Penis with an apical bulb containing epiphallic pore, sometimes expanded and with longitudinal pilasters (*consobrinus*). Penis with (*peregrinus*, *consobrinus*, *kempseyensis*) or without a sheath, internally with small, fleshy, longitudinal pilasters and basal, circular, stimulatory pads (*consobrinus*, *peregrinus*). Penial retractor muscle inserting at the penis/epiphallus junction. Female reproductive system elongate with long vagina and free oviduct. Radula without unusual features except in *kempseyensis*.

DISTRIBUTION AND ECOLOGY

Rhophodon is found from Bairnsdale, Victoria, to the Bulburin State Forest, near Miriam Vale, SEQ. Species have very small ranges. Some are known only from closed forest but others live in fringe rainforest areas and limestone refugia. *R. peregrinus* and *R. consobrinus* are sympatric in the eastern McPherson Ranges, SEQ, and some adjacent areas including the coastal vine thicket at Burleigh Heads, SEQ. Differences in penial morphology between the two species are probably species recognition features. Species live in a variety of microhabitats and have been collected from leaves in litter, under logs, and from moss and litter accummulated on rock surfaces. *R. peregrinus* has also been found in an *Asplenium* fern on a tree.

PATTERNS OF SHELL VARIATION

Size and Shape - *Rhophodon* includes some of the smallest charopids found in eastern Australia with mean shell diameters 1.45–2.66 mm. The largest species, *R. kempseyensis*, is confined to the limestone outcrop between Yessabah and Carrai, west of Kempsey, NSW, where the readily available calcium probably enables greater size. Otherwise size variation appears to be mosaic in nature.

Height is correlated with diameter (mean H/D ratio for the seven species ranges 0.40–0.46) and is reflected in conservative shell shape. Spire protrusion is minimal. Body whorl width shows some reduction in *R. colmani* and *R. minutissimus* correlating with small size. Mean whorl counts range from 4 1/2- to 5-. Species with the largest whorl counts are *R. kempseyensis*; *R. bairnsdalensis* from limestone habitat in southern NSW; and *R. elizabethae* from calcium rich araucarian vine forests of SEQ.

Sculpture - Shell sculpture is complex but variation is relatively simple. The most significant differences are in the number and spacing of the radial ribs and it is possible to divide the species into three groups on this basis - few, bold, widely spaced ribs (*R. bairnsdalensis*, *R. colmani*, Figs 87a, 89a); few, narrower, moderately spaced ribs (*R. minutissimus*, *R. elizabethae*, Figs 81a, 84a); and very many, fine, extremely crowded ribs (*R. peregrinus*, *R. consobrinus*, *R. kempseyensis*, Figs 71a, 74a, 77a). Differences in microsculpture are minor with the more widely spaced microspiral cords of *R. kempseyensis* (Fig. 77c) being an extreme modification which may relate to the larger whorl size of that species. Minor differences occur in number of apical ribs and intensity of apical cording.

Apertural Barriers - Variation in the number of parietal barriers ranges from a single elongate barrier (Fig. 90a) to six barriers and traces (Fig. 71g). The average pattern is for three elongate barriers, expanded posteriorly and deflected downwards.

The average pattern of palatal barriers is for four major barriers to which a superior trace may be added. Major deviations are a single barrier and trace (Fig. 90b, c), three barriers (Fig. 84h) and six barriers (Fig. 87a). In general the barriers are short crescent-shaped lamellae. In *R. colmani* (Fig. 87g) the barriers are expanded with greatly elongate anterior blades.

A columellar barrier may be present and is usually short crescent-shaped and may be supplemented with an accessory trace (Fig. 74i).

PATTERNS OF ANATOMICAL VARIATION

Stability of the *Rhophodon* morphotype, which is evident in the conchological patterns, extends to the anatomy. Apart from differences related to species size e.g. relative lengths of the genital and pallial structures, the most notable variation occurs in the male terminal genitalia.

Male genitalia - Typically the penis has an apical bulb which contains the epiphallic entrance and a main penial chamber with few to several fusiform, longitudinal, fleshy pilasters. Exceptions are *R. consobrinus* (Fig. 75e) and *R. peregrinus* (Fig. 72b) which have altered penial surfaces. These two species are sympatric and the differences in penial morphology are probably species recognition features. The presence of

TABLE 15 - RANGE OF VARIATION IN *RHOPHODON* AND *DISCOCHAROPA* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS (mm)	HEIGHT (mm)	DIAMETER	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Rhophodon peregrinus	16	4 5/8+ (4 3/8–5 1/4+)	0.82 (0.74–0.95)	1.93 (1.79–2.22)	0.43 (0.41–0.47)	—	0.66 (0.62–0.72)	—	156.9 (112–189)	25.93 (18.85–30.44)	0.82 (0.74–0.90)	2.36 (2.22–2.54)
Rhophodon consobrinus	8	4 3/4- (4 3/8–to5 1/8-)	0.94 (0.82–1.07)	2.24 (1.95–2.42)	0.42 (0.40–0.44)	0.03 (0.02–0.04)	0.72 (0.64–0.80)	0.04 (0.03–0.06)	143.4 (109–186)	20.30 (16.93–24.83)	0.88 (0.76–1.07)	2.56 (2.23–2.82)
Rhophodon kempseyensis	11	5 (4 3/4–to5 1/2-)	1.07 (1.03–1.17)	2.66 (2.47–2.98)	0.40 (0.38–0.43)	—	0.86 (0.84–0.92)	—	279.7 (230–330)	33.34 (28.63–38.19)	1.14 (1.03–1.29)	2.33 (2.21–2.44)
Rhophodon elizabethae	9	5- (4 5/8–5 1/4+)	1.10 (0.94–1.24)	2.47 (2.26–2.73)	0.45 (0.41–0.48)	0.09 (0.04–0.13)	0.78 (0.68–0.85)	0.12 (0.05–0.19)	65.2 (52–82)	8.38 (6.93–10.21)	1.01 (0.92–1.13)	2.46 (2.07–2.76)
Rhophodon minutissimus	12	4 1/2+ (4 3/8–4 5/8)	0.70 (0.64–0.76)	1.52 (1.29–1.66)	0.46 (0.40–0.54)	0.04 (0–0.06)	0.53 (0.49–0.55)	0.09 (0.07–0.12)	76.6 (56–98)	16.23 (10.98–21.26)	0.65 (0.60–0.72)	2.35 (2.09–2.59)
Rhophodon colmani	5	4 1/2- (4 1/4–to4 5/8)	0.61 (0.53–0.66)	1.15 (1.34–1.56)	0.42 (0.38–0.46)	0.05 (0.04–0.06)	0.46 (0.43–0.47)	0.11 (0.09–0.14)	26.4 (23–29)	5.81 (5.48–6.51)	0.58 (0.51–0.66)	2.50 (2.38–2.60)
Rhophodon bairnsdalensis	32	5- (4 5/8–5 3/8+)	0.89 (0.76–1.05)	2.06 (1.85–2.42)	0.43 (0.39–0.48)	0.06 (0.00–0.14)	0.64 (0.60–0.72)	0.10 (0.00–0.23)	36.2 (23–57)	5.56 (3.96–8.33)	0.88 (0.74–1.13)	2.37 (2.02–2.66)
Discocharopa aperta	28	3 1/2- (3 1/8–3 3/4)	0.49 (0.39–0.65)	1.12 (0.82–1.46)	0.44 (0.35–0.55)	0.03 (0.02–0.13)	0.32 (0.26–0.40)	0.11 (0.06–0.22)	96.7 (67–114)	31.75 (24.25–40.74)	0.44 (0.34–0.60)	2.41 (2.16–3.31)

a penis sheath correlates with large size and greater intensity of radial ribbing. The epiphallus is normally long and muscular but in *R. kempseyensis* (Fig. 79a) it is very long, correlating with increased whorl count.

Radula - The *Rhophodon* radula shows little interspecific variation reflecting overall similarity in species microhabitats. Size difference between the central tooth and laterals is exaggerated in *R. kempseyensis* (Fig. 78e). The large broad lanceolate mesocone of the laterals is a feature seen in other charopids (Figs 68e, 123h) sympatric with *R. kempseyensis* and appears to be correlated with life on limestone.

COMPARISONS

Rhophodon differs from the conchologically similar *Egilomen* Iredale, 1937 in having apertural barriers and in details of microsculpture. The microspiral cords in *Egilomen* are more prominent than those of *Rhophodon* and are crossed by fine thread-like radials contrasting with the high microradial ribs of *Rhophodon*. Anatomically the pallial configurations of *Rhophodon* and *Egilomen* are distinct. The strongly bilobed condition of the *Egilomen* kidney contrasts with the almost unilobed kidney of *Rhophodon*. Although the penial complexes of the two genera are grossly similar, the tubular penis and stout muscular epiphallus of *Egilomen* are important differences from *Rhophodon*.

KEY TO SPECIES OF *RHOPHODON*

1. Ribs on body whorl very widely spaced (Figs 87a, 89a) 2

 Ribs on body whorl more crowded 3

2. Aperture with three swollen parietal barriers (Fig. 87f) .... *colmani*

 Aperture with a single lamellate parietal barrier (Fig. 90a) .... *bairnsdalensis*

3. Major radial ribs bold, moderately spaced 4

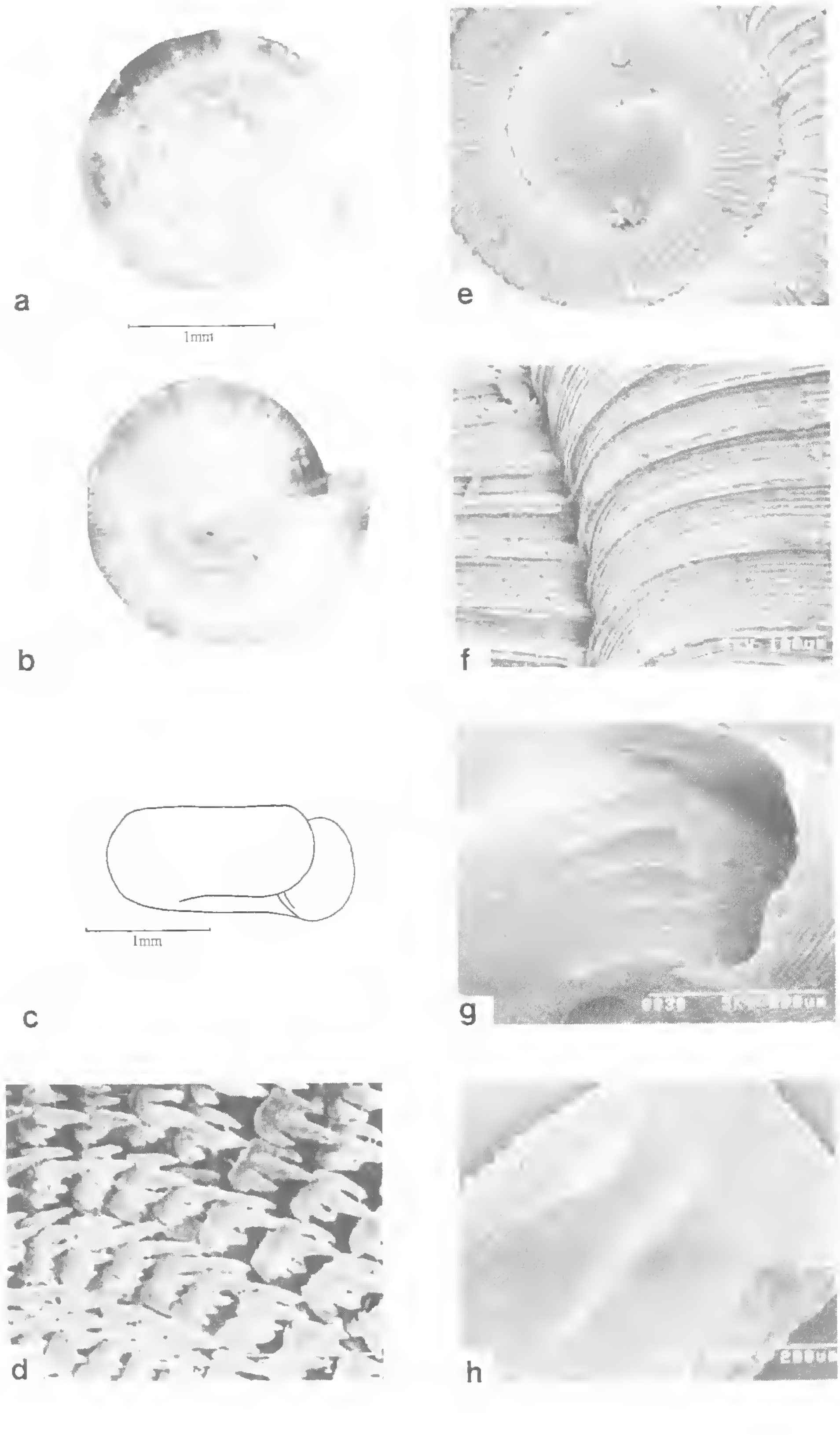
 Major radial ribs finer, very crowded 5

4. Shell very small (mean diameter 1.52 mm); second parietal barrier much shorter than first and third .... *minutissimus*

 Shell larger (mean diameter 2.47 mm), flammulated; second parietal barrier elongate

TABLE 16 - LOCAL VARIATION IN *RHOPHODON PEREGRINUS* HEDLEY, 1924, *RHOPHODON CONSOBRINUS* HEDLEY, 1924, *RHOPHODON KEMPSEYENSIS* SP. NOV. AND *RHOPHODON ELIZABETHAE* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Rhophodon peregrinus												
Tweed River AMC 153719 (Neotype)	1	4 7/8-	0.86	1.99	0.43	—	0.72	—	169	26.98	0.82	2.43
AMC 95838	10	4 5/8 (4 3/8–4 3/4)	0.80±0.012 (0.74–0.86)	1.87±0.016 (1.79–1.97)	0.43±0.006 (0.41–0.47)	—	0.66±0.007 (0.62–0.70)	—	160.4±4.53 (145–189)	27.32±0.592 (24.41–30.49)	0.80±0.253 (0.74–0.86)	2.34±0.030 (2.22–2.50)
Burleigh Heads QMMO 6165	2	5+ (4 7/8–5 1/4+)	0.89±0.065 (0.82–0.95)	2.07±0.155 (1.91–2.22)	0.43	—	0.65±0.010 (0.64–0.66)	—	174	24.95	0.85±0.050 (0.80–0.90)	2.42±0.040 (2.38–2.46)
O'Reillys QMMO 16595	1	4 5/8	0.84	2.03	0.41	—	0.70	—	131	20.49	0.80	2.54
Koreelah S.F. QMMO 10956	1	4 3/8+	0.86	1.89	0.46	—	0.66	—	112	18.85	0.82	2.30
Tooloom Scrub QMMO 10938	1	4 5/8-	0.84	2.05	0.41	—	0.68	—	167	25.87	0.90	2.27
Rhophodon consobrinus												
Richmond River AMC 19922 (Lectotype)	1	4 5/8	0.95	2.18	0.43	0.02	0.74	0.03	116	16.94	0.84	2.59
Burleigh Heads QMMO 16581	1	4 3/8+	0.82	1.95	0.42	0.02	0.64	0.03	109	17.77	0.74	2.57
Mt Warning QMMO 10482	1	4 1/2	0.88	2.20	0.40	0.04	0.68	0.06	117	16.93	0.78	2.82
QMMO 10455	1	4 7/8-	1.07	2.42	0.44	0.04	0.80	0.05	138	18.11	0.88	2.74
Red Scrub F.R. QMMO 10403	1	4 5/8	0.92	2.18	0.42	0.02	0.72	0.03	165	24.11	0.82	2.65
Upper Pine Creek QMMO 16548	3	5- (4 7/8–5 1/8-)	0.96±0.007 (0.95–0.97)	2.33±0.035 (2.26–2.38)	0.41±0.009 (0.40–0.43)	0.03±0.007 (0.02–0.04)	0.72±0.012 (0.70–0.74)	0.40±0.010 (0.03–0.06)	167.3±9.49 (155–186)	22.85±1.09 (21.06–24.83)	0.99±0.044 (0.97–1.07)	2.37±0.068 (2.23–2.44)
Rhophodon kempseyensis												
Natural Arch QMMO 17016 (Holotype)	1	5 1/8+	1.13	2.77	0.41	—	0.92	—	330	37.91	1.17	2.37
QMMO 17015	10	5- (4 3/4—5 1/2-)	1.07±0.014 (1.03–1.17)	2.65±0.043 (2.47–2.98)	0.40±0.004 (0.38–0.43)	—	0.85±0.005 (0.84–0.88)	—	273.5±15.65 (230–312)	32.42±1.679 (28.63±38.19)	1.14±0.025 (1.03–1.29)	2.32±0.023 (2.21–2.44)
Rhophodon elizabethae												
Bobby Range QMMO 17315 (Holotype)	1	5 1/4+	1.11	2.73	0.41	0.04	0.85	0.05	74	8.63	0.99	2.76
QMMO 14717	1	4 3/4	0.94	2.26	0.42	0.04	0.77	0.06	56	7.89	1.09	2.07
QMMO 16858	1	4 5/8	1.11	2.39	0.46	0.09	0.77	0.11	52	6.93	0.95	2.52
QMMO 16590	6	5- (4 3/4—5 1/8)	1.12±0.038 (0.98–1.24)	2.48±0.056 (2.39–2.64)	0.45±0.008 (0.43–0.48)	0.11±0.009 (0.09–0.13)	0.78±0.023 (0.68–0.85)	0.14±0.015 (0.10–0.19)	67.5±3.05 (62–82)	8.67±0.323 (8.09–10.21)	1.01±0.028 (0.92–1.13)	2.46±0.050 (2.32–2.65)


a
1mm
b
c
1mm
d
e
f
g
h

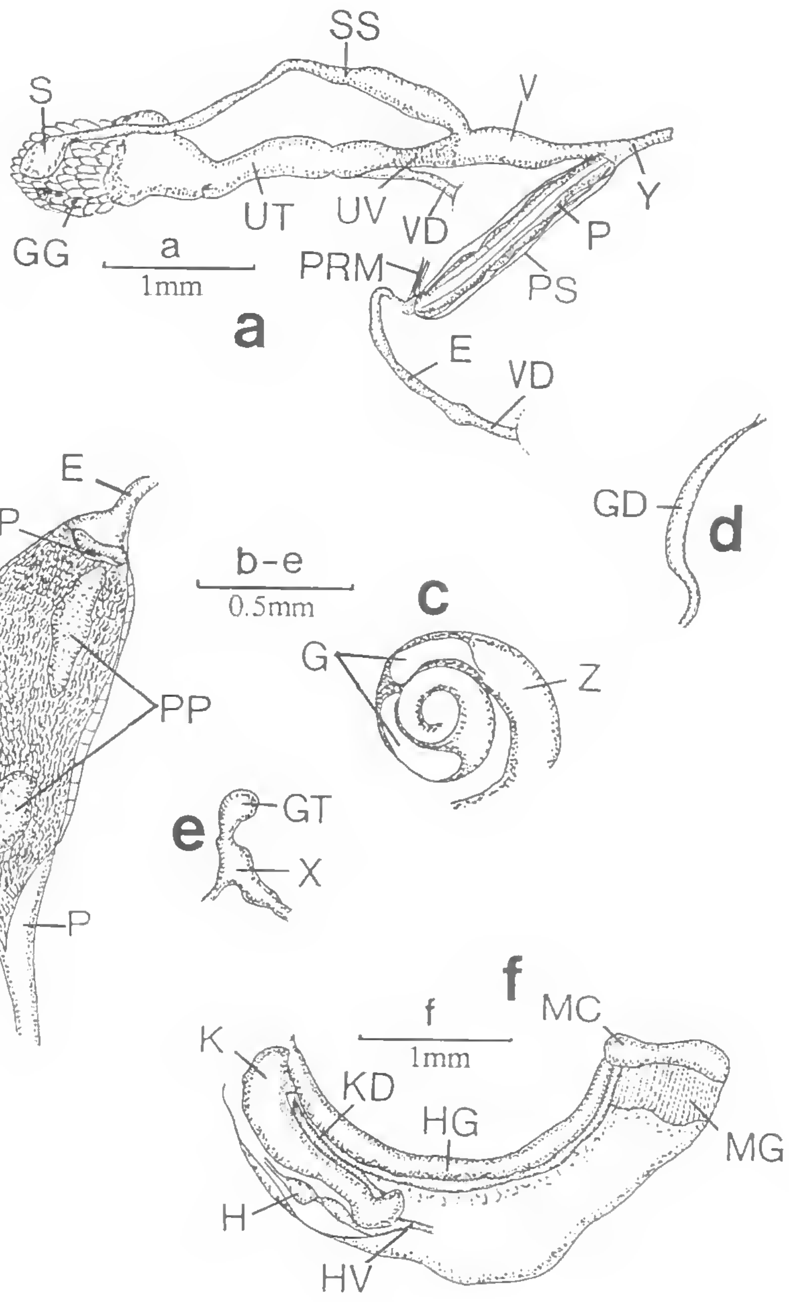


FIG. 72. *Rhophodon peregrinus* Hedley, 1924. On border track c. 6km from O'Reillys, Lamington N.P., SEQ. QMMO16595. a, genitalia; b, penis interior; c, ovotestis; d, hermaphroditic duct; e, talon and carrefour region; f, pallial cavity. Scale lines as marked.

FIG. 71. *Rhophodon peregrinus* Hedley, 1924. a–c, Tweed River, NSW. AMC153719, neotype; d, c. 6km from O'Reilly's on border track, Lamington N.P., SEQ. QMMO16595; e–h, Tweed River, NSW. AMC-95838, paratype. a–c, entire shell; d, marginal teeth; e, apical sculpture; f, post nuclear sculpture; g, parietal barrier; h, palatal barriers. Scale lines as marked.

with an anterior taper; Bobby Range, SEQ ....elizabethae

5.Major radial ribs extremely crowded (mean ribs/mm 33.34); shell larger (mean diameter 2.66 mm)................................*kempseyensis*

Major radial ribs less crowded (mean ribs/mm < 30.00); shell smaller (mean diameter < 2.40 mm)..................................2

6.Parietal barriers consisting of four lamellae and two traces (Fig. 71g); three palatal barriers (Fig. 71h)....................................*peregrinus*

Parietal barriers consisting of three lamellae, and rarely, two traces (Fig. 74h); five palatal lamellae (Fig. 74i).....................*consobrinus*

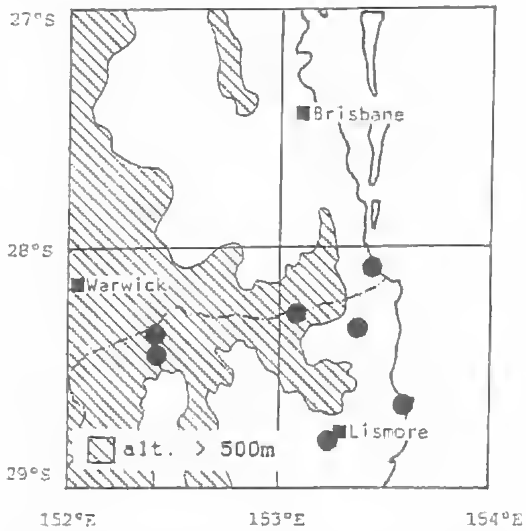


FIG. 73. Distribution of *Rhophodon peregrinus* Hedley, 1924.

Rhophodon peregrinus Hedley, 1924
(Figs 71–73; Tables 15, 16)

Rhophodon peregrinus Hedley, 1924, p. 220, pl. 32, figs 38–40; Iredale, 1937a, p. 329; Iredale, 1941a, p. 268, fig. 6; Iredale, 1941b, p. 2.

COMPARISONS

R. peregrinus is conchologically similar to *R. consobrinus* but is distinguished by the more crowded ribs and slightly depressed spire and greater number of parietal barriers. The two species are sympatric and have quite different penial morphology. These penial surface differences are effective species recognition features.

R. kempseyensis is larger with relatively greater number of whorls and almost twice as many ribs on the body whorl (Fig. 77a). Other *Rhophodon* species have markedly fewer ribs on the body whorl than *R. peregrinus* (Table 15).

PREVIOUS STUDIES

Although Hedley (1924) referred to a type specimen collected by W. Petterd in the Cox collection, the only "type" material of *R. peregrinus* located in the Australian Museum was a lot of 38 specimens (AMC95838) from the type locality, labelled paralectotypes although this designation has no basis in literature. Also in the Australian Museum type collection was a vial labelled "*Rhophodon peregrinus* ... Type lost ...".

TYPE MATERIAL

NEOTYPE AMC153719 (ex AMC95838), Tweed River, NSW. Collected W. Petterd, ex Cox Coll. Height of shell 0.86 mm, diameter 1.99 mm, H/D ratio 0.43, D/U ratio 3.43, whorls 4 7/8-.

OTHER MATERIAL

AMC95838, 37 specimens, same collection data as neotype; Burleigh Heads N.P., SEQ, vine thicket, litter (1, QMMO14116, 6 Jan 1984, J. Stanisic; 25, QMMO6165, Oct 1976, M.J. Bishop); c. 6 km from O'Reilly's, on border track, Lamington N.P., SEQ, NVF, on rocks (7, QMMO16595, 31 Mar 1984, J. Stanisic); Tooloom Scrub, Beaury S.F., NE NSW (28°29'S, 152°24'E) NVF (2, QMMO10938, 15 Mar 1981, AM/QM - ABRS); Burleigh Heads (5, AMC55506, ex J. Brazier); Byron Bay scrub, NSW (2, AMC63847, Lower, ex Cox); Beaury S.F., c. 15 km W of Urbenville, NSW 810 m (28°21'S, 152°24'E) (27, in litter and in *Asplenium* on tree, AMC152160, AMC152161, 18 May 1976, P.H. Colman, I. Loch); Koreelah S.F., c. 12.2 km from Acacia Ck - Killarney Rd, NSW SEVT/MVF (28°21'S, 152°24'E) (4, QMMO10956, AMC128559, 15 Mar 1981, AM/QM - ABRS); Richmond Rv, Lismore, NSW, in scrub under decayed leaves and dead timber (3, AMC63872, ex Brazier).

DIAGNOSIS

Shell minute, diameter 1.79–2.22 mm (mean 1.93 mm) with 4 3/8 to 5 1/4+ (mean 4 5/8+) tightly coiled whorls, the last descending more rapidly. Apex and early spire depressed to strongly depressed. Height of shell 0.74–0.95 mm (mean 0.85 mm). H/D ratio 0.41–0.47

(mean 0.43). Protoconch exsert, 1 1/2 to 1 3/4 whorls, mean diameter 410.9 μm at 1 1/2 whorls. Apical sculpture (Fig. 71e) of curved, broad radial ribs and weak spiral wrinkles, ribs becoming more crowded toward the nuclear/post nuclear junction. Postnuclear sculpture (Fig. 71f) of numerous, very crowded, high, slightly protractively sinuated radial ribs, 112–189 (mean 156.9) ribs on the body whorl. Ribs/mm 18.85–30.44 (mean 25.93). Apices of ribs with spiral sculpture. Microsculpture (Fig. 71f) of fine radial riblets and conspicuous low spiral cords which are raised at their junction with the radial riblets producing a beaded effect. Umbilicus (Fig. 71b) wide, cup-shaped, diameter 0.74–0.90 mm (mean 0.82 mm). D/U ratio 2.22–2.54 (mean 2.36). Sutures impressed; whorls shouldered above and rounded below a weakly rounded periphery. Aperture ovately lunate. Numerous barriers present. Parietal barriers (Fig. 71g) consisting of four crescent-shaped lamellae and two thread-like traces. First barrier large, deflected upwards; second, third and fourth without marked anterior taper, directed downwards. Superior and inferior traces may be present. Palatal barriers consisting of three crescent shaped lamellae (Fig. 71h) and a superior trace (Fig. 71g) high up on the palatal margin. Columellar barrier small, thread-like. Lip simple, columella not expanded or reflected. Parietal callus developed. Colour white to straw-yellow with brown radial streaks and suffusions. Based on 16 measured adults.

Genitalia with vas deferens/epiphallus junction (Fig. 72a) complex, valvular. Epiphallus (Fig. 72a) a muscular tube continuing to the penis head where its coils before entering the penis apically. Penis (Fig. 72a) an almost cylindrical, muscularised tube with a thin sheath and head slightly expanded, tapering as it nears the atrium, internally with a simple epiphallic entrance (Fig. 71b) surrounded by a muscular collar. Interior of the penis with large, apical, longitudinal pilaster, a basal doughnut-shaped pilaster, and general wall sculpture of spongy pustulations.

Radula (Fig. 71d) typical.

Based on 5 dissected adults (QMMO16595).

Range and Habitat

Cool subtropical notophyll vine forests of the McPherson Ranges, SEQ, westward to the Great Dividing Range on the NSW/QLD border; coastal rainforests at Byron Bay, NSW and Burleigh Heads, SEQ. An early record at Lismore, NSW, needs to be confirmed. *R. peregrinus* has been collected in litter, among moss on rocks, among accumulated debris, and unusually, in an epiphytic fern growing on a tree.

Remarks

Lack of material makes a study of interpopulational variation impossible at this stage. However, a single specimen (Table 16) from the Koreelah State Forest, NSW, in the western part of its range, differs in rib spacing from specimens further east.

Rhophodon consobrinus Hedley, 1924
(Figs 74–76; Tables 15, 16)

Rhophodon consobrinus Hedley, 1924, p. 220, pl. 31, figs 32-34; Iredale, 1937a, p. 329; Iredale, 1941b, p. 2.

Comparisons

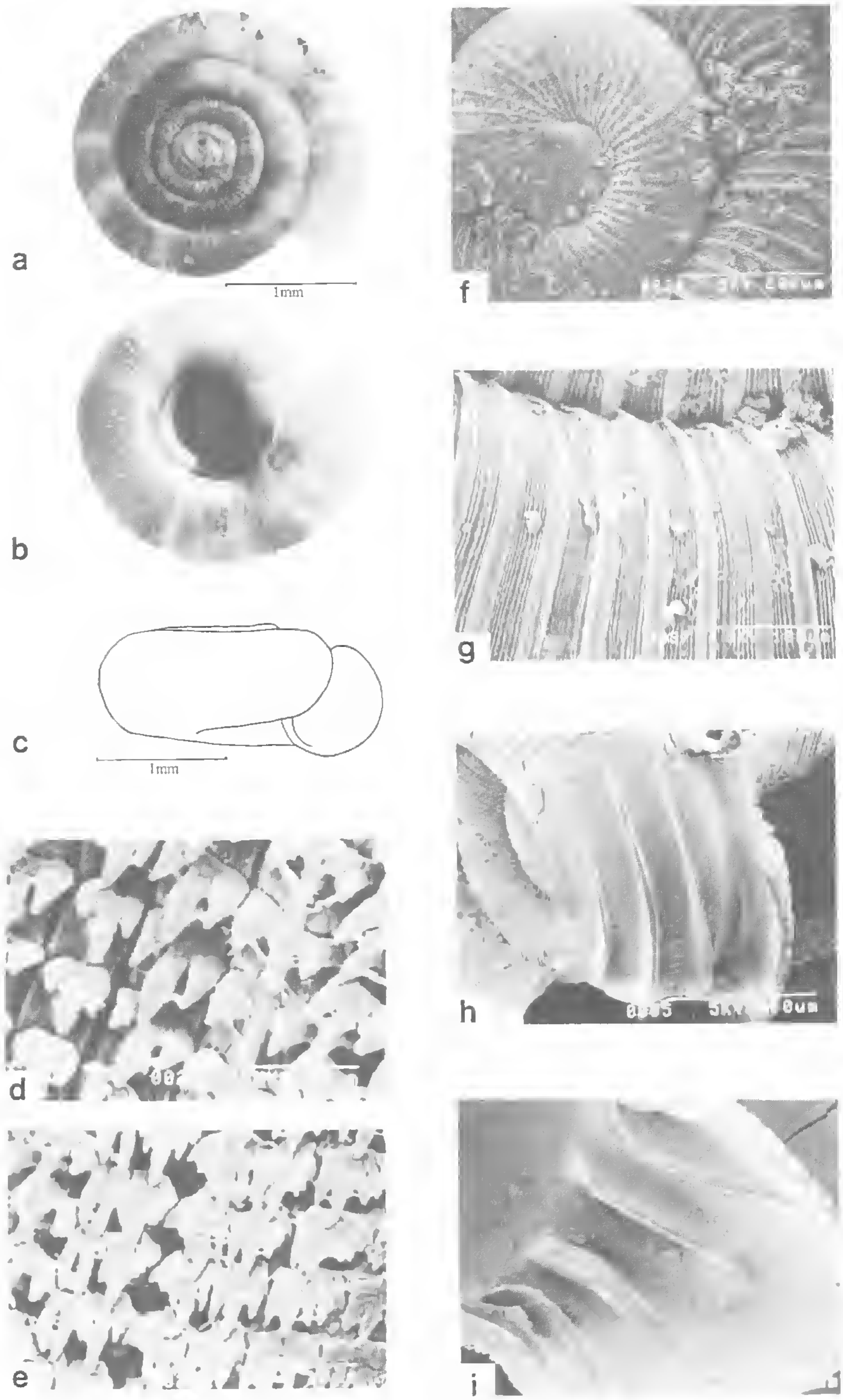
R. consobrinus can be distinguished from *R. peregrinus* by its modified penis which has the apical bulb reflexed and expanded to include longitudinal pilasters (Fig. 75c). Conchological differences are minor except for the disposition of apertural barriers. *R. consobrinus* (Fig. 74h) has fewer parietal barriers than *R. peregrinus* (Fig 71g). *R. kempseyensis* (Fig. 77a), has almost twice as many ribs on the body whorl, is larger and has a higher whorl count than *R. peregrinus*. Other species can be differentiated by their smaller rib counts (Table 15).

Type Material

Lectotype: AMC19922, Richmond River, NSW. Presented W.F. Petterd. Height 0.95 mm., diameter 2.18 mm., H/D ratio 9.43, D/U ratio 2.59, whorls 4 5/8.

Other Material

Burleigh Heads N.P., SEQ, vine thicket (7, QMMO16581, 29 Sept 1986, J. Stanisic, J. Chaseling; 2, QMMO6160, Nov 1976, M.J. Bishop; under logs, 7, QMMO16922, 21 Jan 1987, J. Stanisic, D. Potter): Upper Pine Creek, Canungra, SEQ. NVF/Araucaria (on rocks, 20, QMMO16548, 1 Oct 1986, J. Stanisic, D. Potter; on moss covered rock, 7, QMMO16906, 21 Jan 1987, J. Stanisic, D. Potter; under logs, 7, QMMO16586, 29 Sept 1986, J. Chaseling, J. Stanisic); Binna Burra, Lamington N.P., SEQ. (28°12'S, 153°11'E) NVF/Palms (1. QMMO10446, 18 Mar 1981, AM/QM - ABRS); Red Scrub Flora Reserve, Whian Whian S.F., NSW, 210 m (28°38'S, 153°19'E) (1. AMC152157, 15 May 1976, P.H. Colman, I.


a
1mm
b
c
1mm
d
e
f
g
h
i

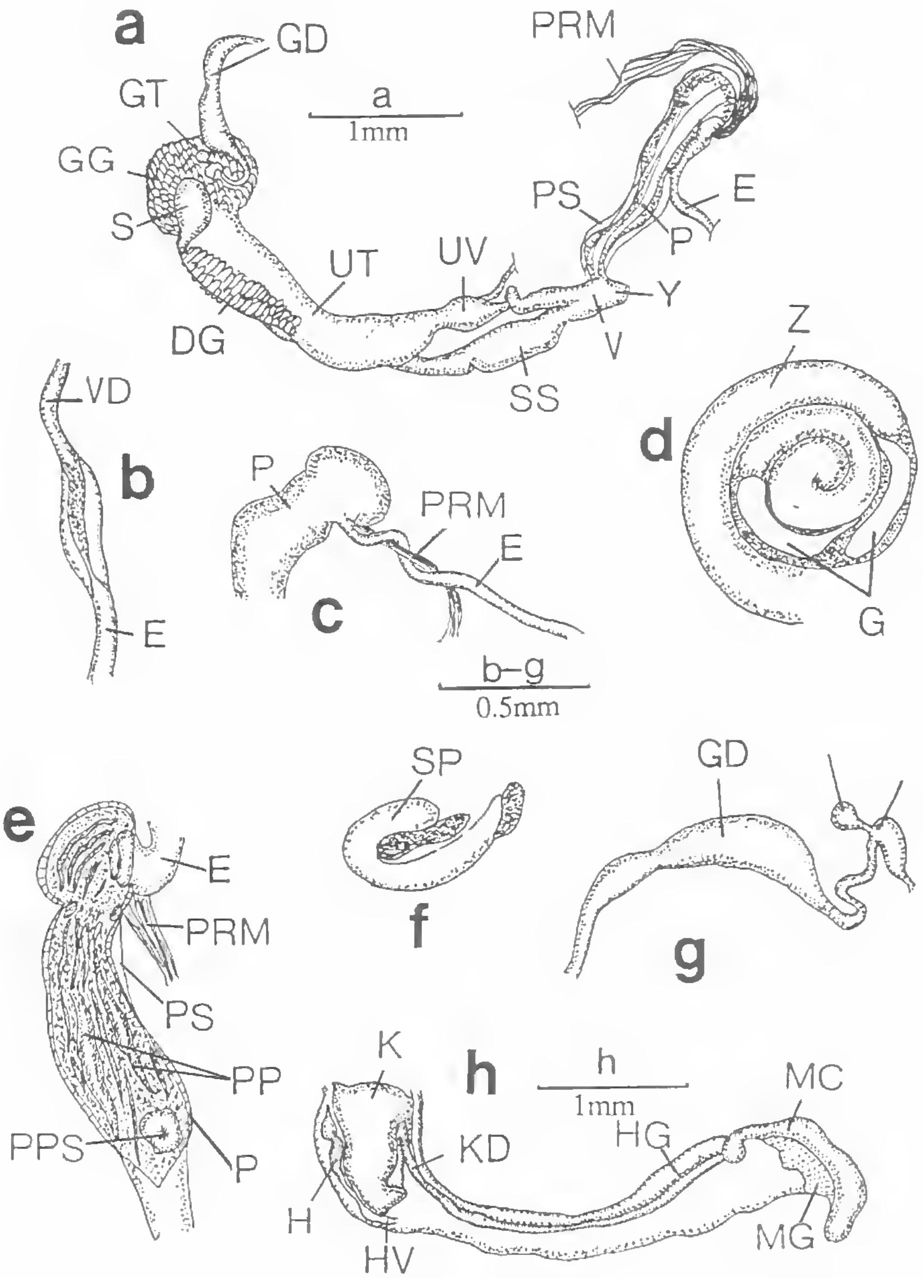


FIG. 75. *Rhophodon consobrinus* Hedley, 1924. a–e, g, h, Upper Pine Ck, Canungra, SEQ. QMMO16548, QMMO16586, QMMO16906. f, Burleigh Heads N.P., SEQ. QMMO16581. a, genitalia; b, vas deferens - epiphallus junction; c, details of penis - epiphallus junction; d, ovotestis; e, penis interior; f, spermatophore; g, talon, hermaphroditic duct and carrefour region; h, pallial cavity. Scale lines as marked.

FIG. 74. *Rhophodon consobrinus* Hedley, 1924. a–c, Richmond River, NSW. AMC19922, lectotype; d–e, h–i, Upper Pine Creek, Canungra, SEQ. QMMO16906, QMMO16548; f–g, Natural Bridge N.P., SEQ. QMMO10455. a–c, entire shell; d, central and lateral teeth; e, marginal teeth; f, apical sculpture; g, post nuclear sculpture; h, parietal barriers; i, palatal barriers. Scale lines as marked.

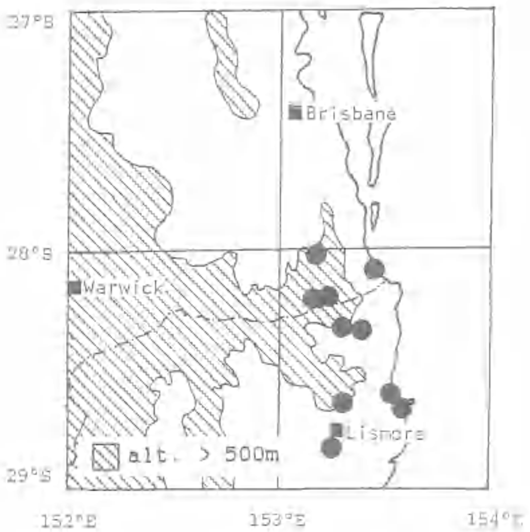


FIG. 76. Distribution of *Rhophodon consobrinus* Hedley, 1924.

Loch); Rocky Ck., Red Scrub Flora Reserve, NSW (28°38'S, 153°19'E) rainforest (5, QMMO10403, AMC128864, AM/QM - ABRS); Tyagarah (1, AMC152158, Lower, ex Cox); Tweed River, NSW (3, AMC5310, ex Cox); Cape Bryon, NSW (1, AMC140480, 1 May 1958, L. Price); upper Tweed River, NSW (1, AMC152159, Petterd, ex Cox); Natural Bridge N.P., NSW, NVF (28°13'S, 153°14'E) (QMMO10455, AMC129268, 18 Mar 1981, AM/QM - ABRS); Richmond Rv, Lismore, NSW, in scrub under decayed leaves and dead timber (1, AMC63872, ex Brazier).

DIAGNOSIS

Shell minute, diameter 1.95–2.43 mm (mean 2.35 mm) with 4 3/8+ to 5 1/8- (mean 4 3/4-) tightly coiled whorls, the last descending more rapidly. Early spire and apex weakly to moderately depressed (Fig. 74a). Height of shell 0.82–1.07 mm (mean 0.94 mm), H/D ratio 0.40-0.44 (mean 0.42). Protoconch exsert, of 1 1/2 to 1 5/8 whorls, mean diameter 457.0 μm at 1 1/2 whorls. Apical sculpture (Fig. 74f) of curved, broad radial ribs, becoming more crowded toward the nuclear/postnuclear shell junction, and weak spiral wrinkles. Postnuclear sculpture (Fig. 75g) of numerous, crowded, broad, slightly protractively sinuate radial ribs, 109–186 (mean 143.4) ribs on the body whorl. Ribs/mm 16.93–24.83 (mean 20.30). Apices of ribs rounded and sculptured with radial lines. Microsculpture (Fig. 74g) of fine radial riblets, 5–9 between each pair of major ribs, and very low spiral thickenings, which are raised at their junction with the radial riblets to form elongate beads. Umbilicus (Fig. 74b) wide, cup-shaped, diameter 0.76–1.07 mm (mean 0.88mm). D/U ratio 2.23–2.82 (mean 2.56). Sutures impressed. Whorls (Fig. 74c) rounded below and shouldered above a slightly compressed periphery. Aperture ovately lunate. Numerous barriers present, extending posteriorly for about 1/8 whorl. Parietal barriers (Fig. 74h) three, long, crescent-shaped lamellae, and several, variable, thread-like traces. First and second parietals large, crescent-shaped, second deflected downwards; third low, directed downwards. Parietal traces may occur above the first parietal lamella and between the first and second parietal. Palatal barriers (Fig. 74c) five, the fifth crescent-shaped almost touching the first parietal; fourth, almost equal in size to the fifth, also crescent shaped; third smaller, crescent-shaped, sometimes bifid apically; second and first basal, thin, small. A superior palatal trace may be present at the parieto-palatal margin (Fig. 74h). Columellar lamella small. Lip simple, columella not expanded or deflected. Parietal callus developed.. Colour light straw-yellow with reddish-brown radial streaks and suffusions. Based on 8 measured adults.

Genitalia with penial retractor muscle inserted at epiphallus/penis junction (Fig. 75a). Penis (Fig. 75e) tubular, reflexed c. 1/3 way along its length, with a thin sheath, and complex internal sculpture. Epiphallus entering penis through two thickened lips (Fig. 75e) adjacent to several high longitudinal pilasters. Remainder of penis chamber wall with broad low pustules giving way to low thin ridges basally. Base of the lower chamber with a stimulatory doughnut-like pad. Spermatophore (Fig. 75f) hook-shaped.

Radula (Fig. 74d,e) similar to that of *R. peregrinus*.

Based on 13 dissected specimens (QMMO-16548, QMMO16581, QMMO16906, QMMO-16922, QMMO16586).

RANGE AND HABITAT

Moist, warm lowland notophyll vine forests of the Big Scrub area, northern NSW and eastern McPherson Ranges and the coastal vine scrubs at Byron Bay, NSW, and Burleigh Heads, SEQ. *R. consobrinus* has been collected in litter, under logs and on moss covered rocks.

REMARKS

Although *R. peregrinus* and *R. consobrinus* have not been found microsympatrically, their overlapping ranges and convergent microhabitat preferences make this a distinct possibility. Certainly, penial differences suggest microsympatry.

Rhophodon kempseyensis sp. nov.
(Fig. 77–80; Tables 15, 16)

ETYMOLOGY

For the Kempsey region.

COMPARISONS

This species is recognizable by its lustrous golden brown shell which has numerous, extremely crowded radial ribs. It has the highest rib count of any east Australian charopid. The species closest to *R. kempseyensis* are *R. peregrinus* and *R. consobrinus* but they have only c. half the number of ribs on the body whorl, are smaller, and have relatively fewer whorls (Table 15). *Letomola contortus* which is sympatric with *R. kempseyensis*, has a wide umbilicus and two apertural barriers - one basal and one parietal (Fig. 68a, b). Sculpturally *L. contortus* differs from *R. kempeyensis* in having a more bulbous protoconch (Fig. 67d) with irregular malleations and ridges, and adult whorls (Fig. 67e, f) with low, broad radial ridges and weak spiral cords.

TYPE MATERIAL

HOLOTYPE: QMMO17016, Natural Arch, Carrai S.F., NSW. 30°59'S, 152°21'E, limestone, on mossy rocks. Collected by J. Stanisic, D. Potter, P.H. Colman, 3 Mar 1987. Height of shell 1.13mm, diameter 2.77. H/D ratio 0.41, D/U ratio 2.37, whorls 5 1/8+.

PARATYPES: QMMO17015, 106 specimens, same collection data as holotype; Limestone caves at Natural Arch, W. of Kempsey, NSW (30°59'S, 152°21'E) (150+, AMC153720, 10 Mar 1981, W.Ponder, O. Griffiths); Haydonville, W. of Kempsey, S. side of 'Natural Arch', under rock overhang (4 specimens, AMC152156, 20 Jan 1982, ex A.B. Rose, M. Dodkin); Yessabah Cave, W. of Kempsey, in leaf and soil litter (31°06'S, 152°42'E) (50+ specimens, AMC119351, 9 Oct 1979, J. Stanisic, P.H. Colman), Natural Arch, Carrai Caves, litter (70+ specimens, AMC152155, 22 Feb 1980, P.H. Colman).

DIAGNOSIS

Shell minute, diameter 2.47–2.98 mm (mean 2.66 mm) with 4 3/4- to 5 1/2- (mean 5) tightly coiled whorls. Spire and apex depressed, last whorl descending more rapidly. Height 1.03–1.17 mm (mean 1.07 mm), H/D ratio 0.38–0.43 mm (mean 0.40 mm). Protoconch of 1 1/2 to 1 5/8 whorls, exsert, mean diameter 449.8 μm at 1 1/2 whorls. Apical sculpture (Fig. 77d) of curved radial riblets, more crowded at nuclear-post nuclear boundary, and fine spiral wrinkles. Post-nuclear sculpture (Fig. 77e) of numerous, crowded, protractively sinuated radial ribs, 230–330 (mean 297.7) ribs on the body whorl. Ribs/mm 28.63-38.19 (mean 33.34). Microsculpture (Fig. 77e) of crenulate radial riblets, 2-3 between each pair of major ribs and very low, widely spaced, rather inconspicuous spiral cords, raised at their junction with the microradials to produce a weak beaded effect, continuous on the apices of the radial ribs. Umbilicus (Fig. 77b) wide, cup-shaped, diameter 1.03–1.29 mm (mean 1.14 mm). D/U ratio 2.21–2.44 mm (mean 2.33 mm). Sutures impressed. Whorls rounded above and below the periphery (Fig. 77c), shouldered at the upper margin, flattened below. Aperture ovately lunate with seven barriers. Four palatal barriers (Fig. 78a), fourth and third large crescent-shaped; second smaller, crescent-shaped at the basal margin; first similar in size to second, situated at the baso-columellar margin. Three parietal barriers (Fig. 78b). First and second elongate crescent-shaped lamellae; third a low elongate blade. Lip simple, columella not thickened, almost vertical, not reflected. Parietal callus present. Colour light straw-yellow with broad reddish-brown radial streaks and suffusions. Based on 11 measured adults.

Genitalia with vas deferens/epiphallus junction valvular. Epiphallus (Fig. 79a) long, thick muscular, coiled; internally with longitudinal thickenings, entering penis apically through thickened pilasters (Fig. 79b). Penis (Fig. 79b) a long, muscular tube with a thin sheath, internally with a primary longitudinal pilaster, a medial, spherical thickening and secondary, smooth longitudinal thickenings. Penial retractor muscle short, originating from the diaphragm and inserting on the epiphallus just prior to its entry into the penis. Spermatophore (Fig. 79f) hook-shaped.

Radula (Fig. 78e, f) with very long lanceolate mesocone on laterals.

Based on three dissected adults (QMMO-17015).

RANGE AND HABITAT

Limestone outcrops between Yessabah and Carrai, west of Kempsey, NSW in evergreen vine thicket derived from the surrounding warm temperate rainforests. Live specimens have

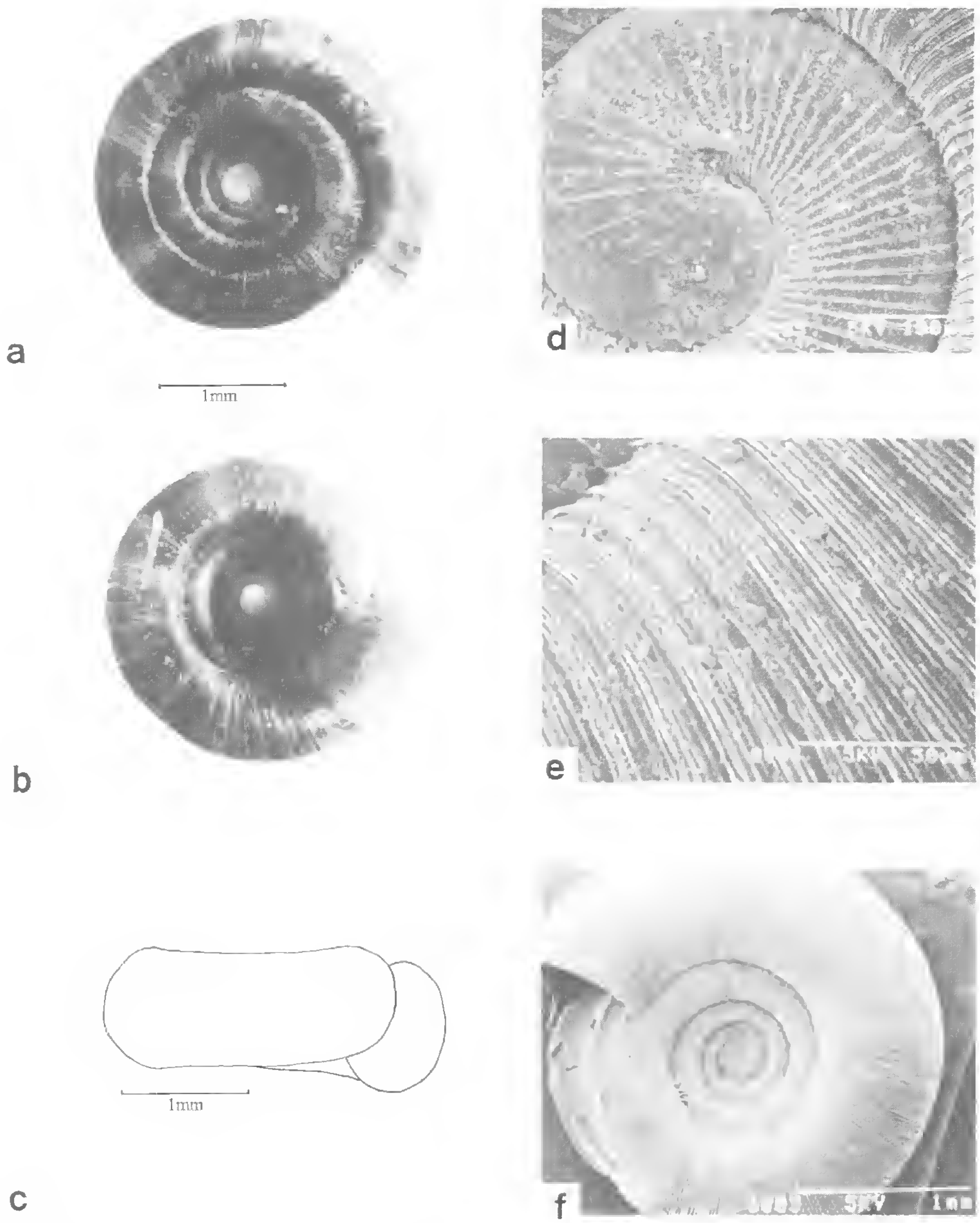


FIG. 77. *Rhophodon kempseyensis* sp. nov. a–c, Natural Arch, Carrai S.F., NSW. QMMO17016, holotype; d–f, same data holotype. QMMO17015, AMC153720, paratypes. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, base. Scale lines as marked.

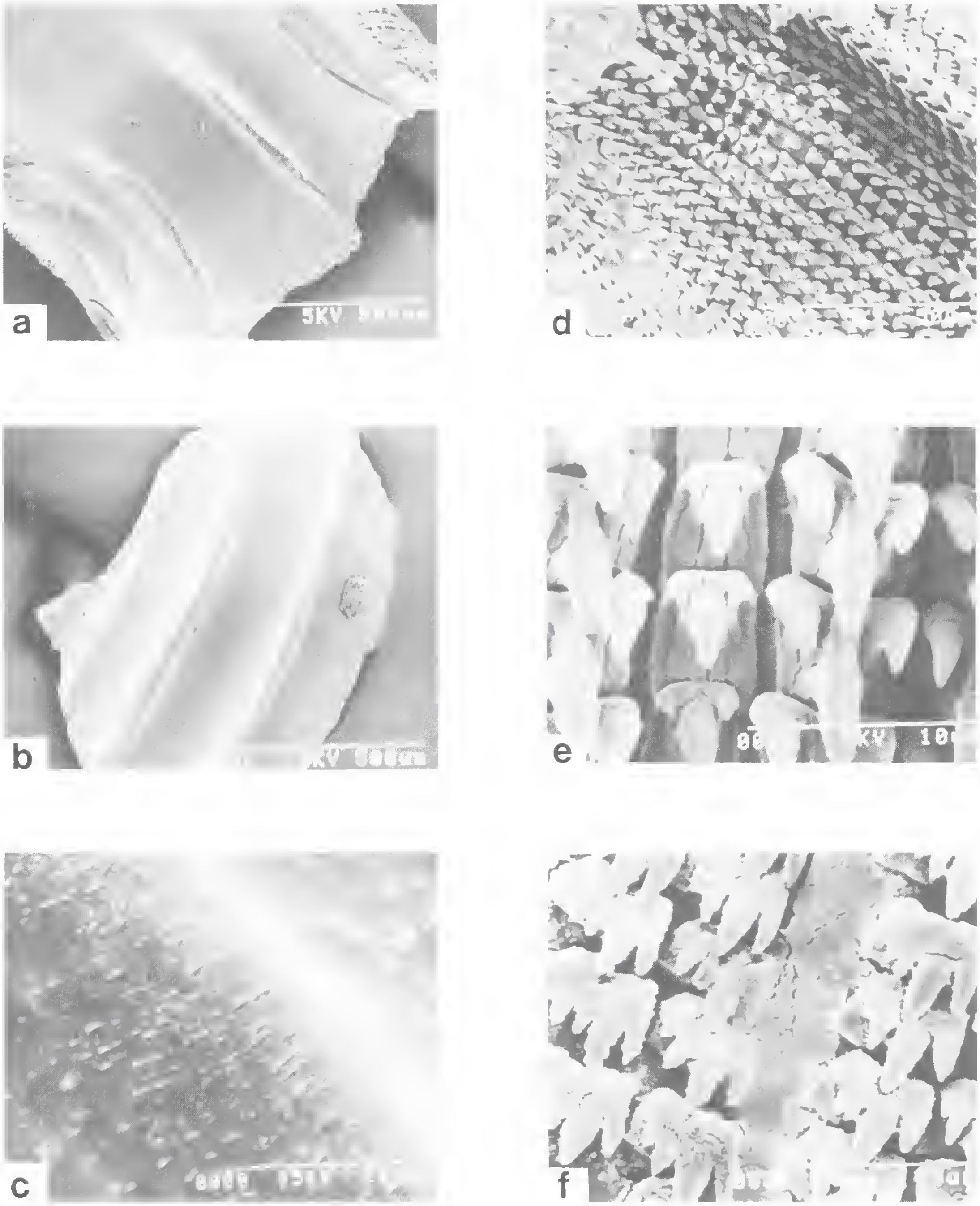


FIG. 78. *Rhophodon kempseyensis* sp. nov. Natural Arch, Carrai S.F., NSW. QMMO17015, paratype. a, palatal barriers; b, parietal barriers; c, microdenticulation on surface of third palatal barrier; d, radula; e, central and lateral teeth; f, marginal teeth. Scale lines as marked.

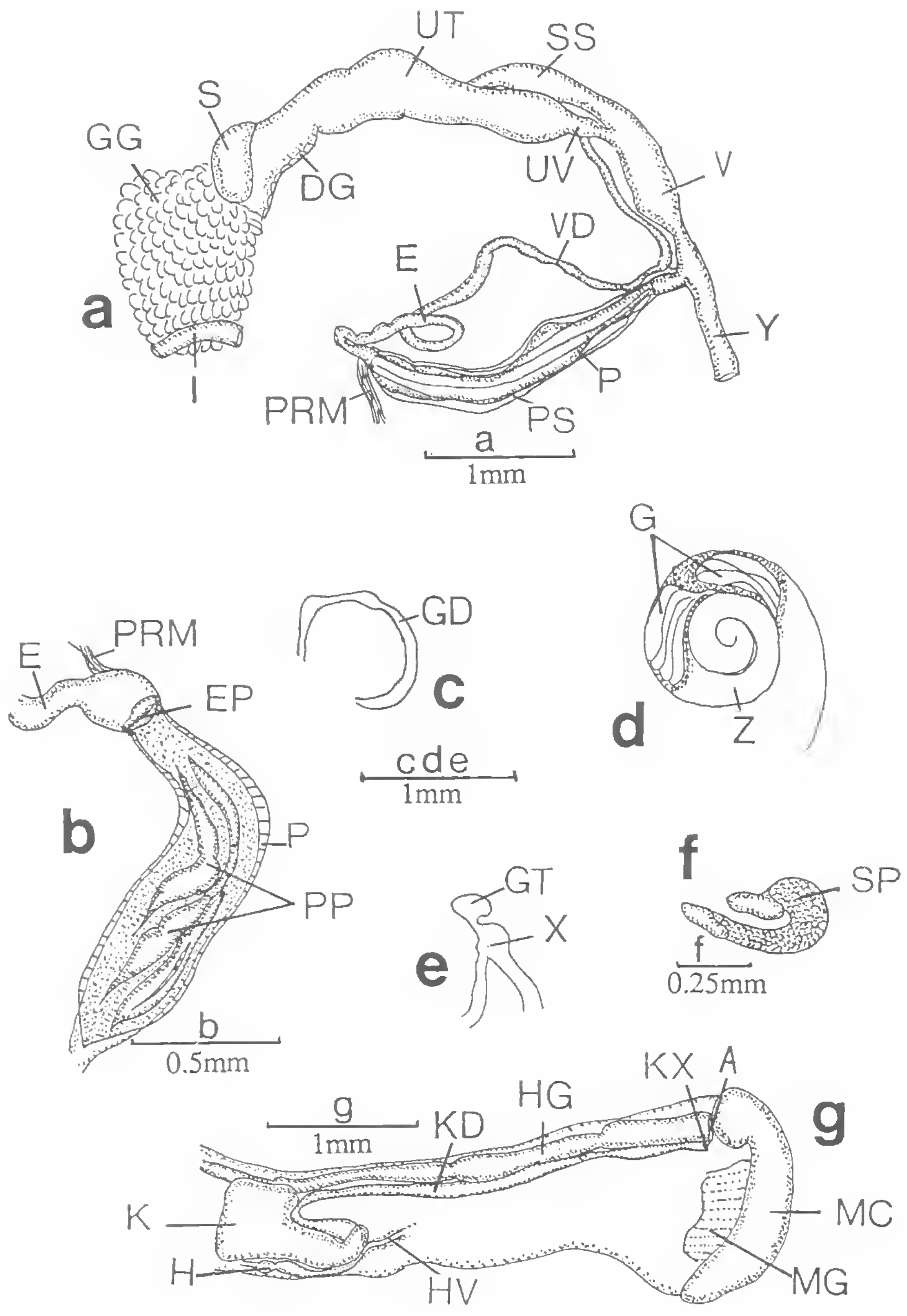


FIG. 79. *Rhophodon kempseyensis* sp. nov. Natural Arch, Carrai S.F., NSW. QMMO17015, paratype. a, genitalia; b, penis interior; c, hermaphroditic duct; d, ovotestis; e, talon and carrefour; f, spermatophore; g, pallial cavity. Scale lines as marked.

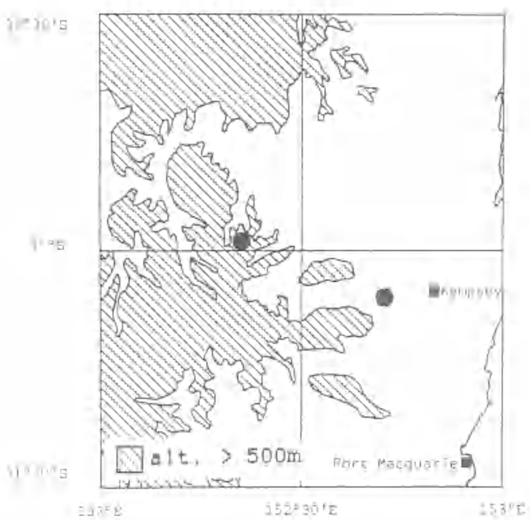


FIG. 80. Distribution of *Rhophodon kempseyensis* sp. nov.

been collected from the surface of mossy limestone rocks.

REMARKS

The lateral teeth in which the mesocone is conspicuously large, are similar to those in the sympatric *Letomola contortus* and *Coenocharopa yessabahensis* which also have been collected live on the limestone rocks. This convergence may reflect similar feeding habits. *R. kempseyensis* is closely related to *R. peregrinus* and *R. consobrinus* probably derived by habitat fragmentation.

Rhophodon elizabethae sp. nov

(Figs 81–83: Tables 15, 16)

ETYMOLOGY

For Elizabeth Chaseling.

COMPARISONS

Small size, flammulated shell with bold radial ribs, wide umbilicus and number of apertural barriers distinguish this species from any sympatric charopid species. *R. minutissimus* is most similar to *R. elizabethae* but has fewer whorls, smaller umbilicus, and a smaller monochrome golden brown shell. In addition *R. elizabethae* (Fig. 81h) has a greater number of palatal barriers and, unlike *R. minutissimus* (Fig. 34g,h), does not have the second parietal barrier shortened.

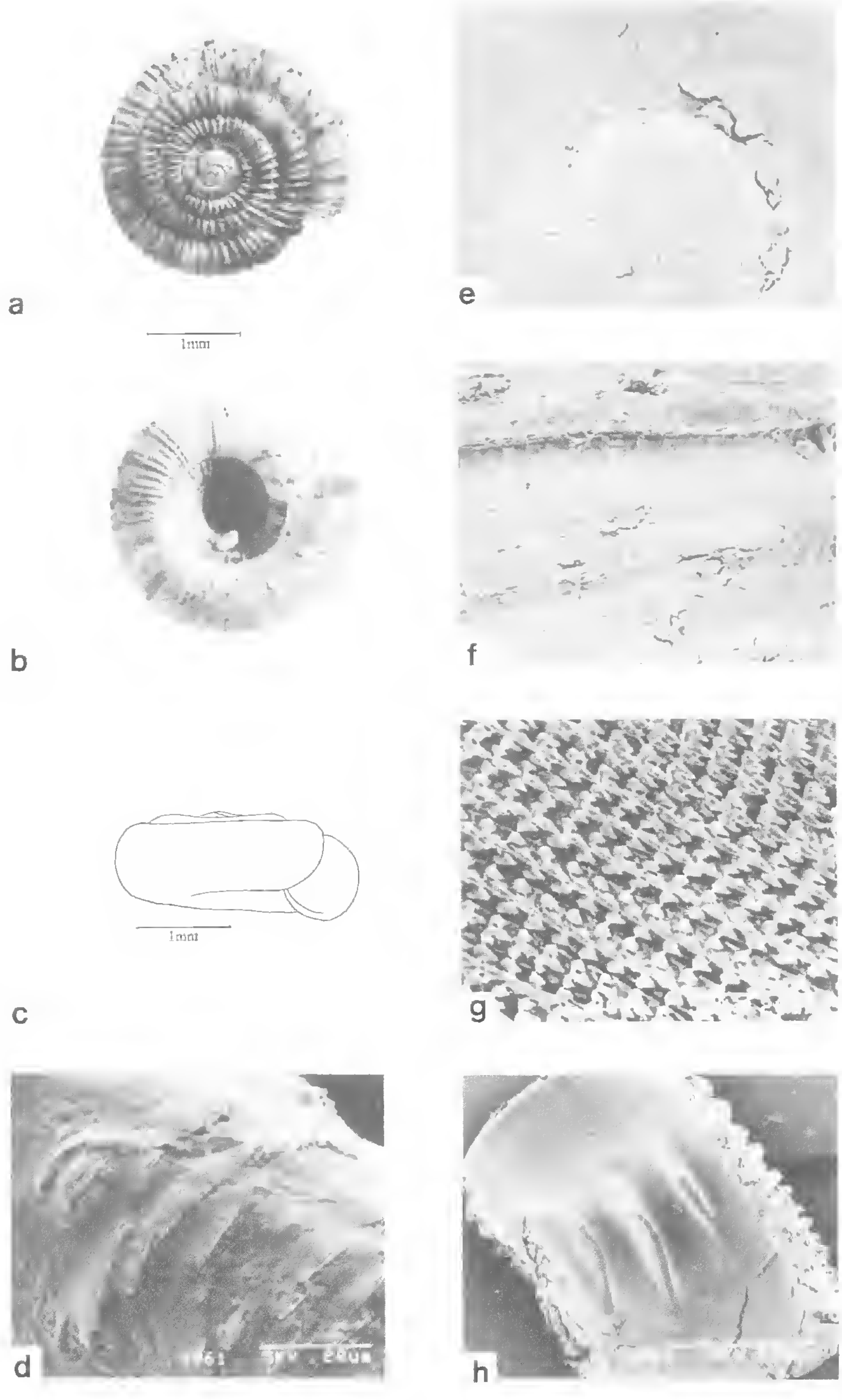
TYPE MATERIAL

HOLOTYPE: QMMO17315, Granite Creek, foothills of Bobby Range, SEQ. 24°30.7'S, 151°30.3'E, under leaf litter. Collected by T. Carless, 7 Dec 1983. Height of shell 1.11 mm, diameter 2.73 mm, H/D ratio 0.41, D/U ratio 2.76, whorls 5 1/4+.

PARATYPES: QMMO14714, 1 specimen, same data as holotype; summit Mt Booroon Booroon, SW of Miriam Vale, SEQ, MVF/*Araucaria*, litter, on and among rocks (17, QMMO16590, QMMO16858, 17 Sept 1985, J. Stanisic, D. Potter); base, Mt Booroon Booroon, SEQ, NVF along creek, under logs (3, QMMO16592, 17 Sept 1985, J. Stanisic, D. Potter).

DIAGNOSIS

Shell minute, diameter 2.26–2.73 mm (mean 2.47 mm), with 4 3/8 to 5 1/4+ (mean 5-) tightly coiled whorls, last descending slightly. Apex and early spire (Fig. 81a) flat to very slightly elevated, SP/BWW ratio 0.05–0.19 (mean 0.12), height 0.94–1.24 mm (mean 1.10 mm). H/D ratio 0.41–0.48 (mean 0.45). Protoconch of 1 5/8 to 1 3/4 whorls, mean diameter 520.1 μm at 1 1/2 whorls. Apical sculpture (Fig. 81e) of curved radial ribs, becoming more crowded at the nuclear-post nuclear junction. Post nuclear sculpture (Fig. 81f) of bold, widely spaced, protractively sinuated radial ribs, 52–82 (mean 65.2) ribs on the body whorl. Ribs/mm 6.93–10.21 (mean 8.38). Microsculpture (Fig. 81f) of fine, thread-like radial riblets, 10–18 between each pair of major ribs, and fine crowded, spiral cords which are continuous on the apices of the radial ribs. Umbilicus (Fig. 81b) wide, cup-shaped, diameter 0.92–1.13 mm (mean 1.01 mm). D/U ratio 2.07–2.76 (mean 2.46). Sutures impressed, whorls rounded below and strongly shouldered above a slightly flattened periphery (Fig. 81c). Aperture ovately lunate with three parietal, five palatal and one columellar barrier. Parietal barriers blade-like, consisting of two lamellae and an elongate, thread-like superior trace. First barrier elongate, crescent-shaped, abruptly tapered at each end; second with anterior taper and an expanded, downwardly deflected, posterior section. Columellar barrier low, crescent-shaped, horizontal. Five palatal barriers (Fig. 81h) consisting of four lamellae and one trace. Lamellae short, expanded. Superior trace sometimes present, short, close to the palato-parietal margin. Lip simple; columella without noticeable thickening. Parietal callus developed. Colour light straw-yellow with variable brown radial streaks and suffusions. Based on 9 measured adults.


a
1mm
b
c
1mm
d
e
f
g
h

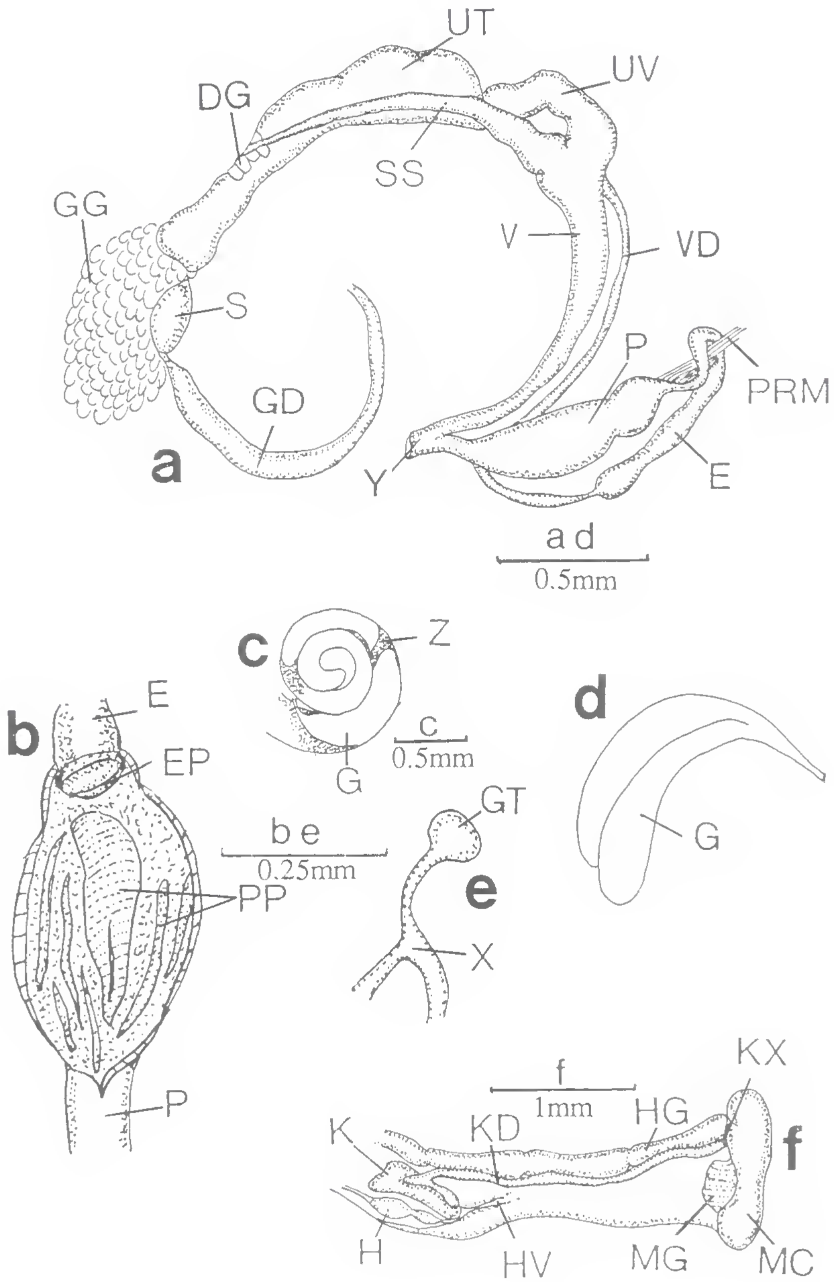


FIG. 82. *Rhophodon elizabethae* sp. nov. Summit, Mt Booroon Booroon, SW of Miriam Vale. SEQ. QMMO16590, paratype. a, genitalia; b, penis interior; c, hermaphroditic duct; d, ovotestis; e, pallial cavity. Scale lines as marked.

FIG. 81. *Rhophodon elizabethae* sp. nov. a–c, Granite Creek, foothills of Bobby Range, SEQ. QMMO17315, holotype; d–h, Summit, Mt Booroon, Booroon, SW of Miriam Vale, SEQ. QMMO16590, QMMO16858, paratypes. a–c, entire shell; d, microdenticulations on parietal barrier; e, apical sculpture; f, post nuclear sculpture; g, radula; h, palatal barriers. Scale lines as marked.

Genitalia with epiphallus (Fig. 82a) reflexed before entering the penis apically through a simple pore (Fig. 82b) surrounded by a fleshy pilaster. Penis (Fig. 82b) simple with apical bulb containing epiphallic entrance and lower chamber containing a single large, spongy, longitudinal pilaster, several shorter pilasters, and low pustules. No penial sheath. Penial retractor muscle a short tuft inserting apically on penial bulb adjacent to epiphallus.

Radula (Fig. 81g) typical.

Based on 2 dissected adults (QMMO16590).

RANGE AND HABITAT

Under logs, on rocks and amongst litter in moist notophyll vine forest of the Bobby Range, SEQ.

REMARKS

R. elizabethae has a very restricted range compared to other charopids. Its closest relative appears to be *R. minutissimus*.

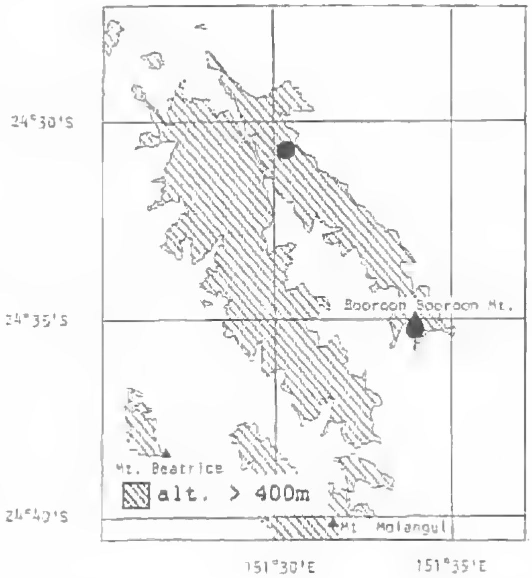


FIG. 83. Distribution of *Rhophodon elizabethae* sp. nov. in the Bobby Range area, SEQ.

Rhophodon minutissimus sp. nov.
(Figs 84–86: Tables 15, 17)

ETYMOLOGY

Latin *minutus*, little; for the small size.

TYPE MATERIAL

HOLOTYPE: QMMO17316, c. 1 km S of Raynbird Creek Rd. on Lacey's Creek Rd, Lacey's Creek, SEQ 27°14'S, 152°43'E. Collected AM/QM-ABRS, 30 Sept 1982. Height of shell 0.70 mm, diameter 1.29 mm, H/D ratio 0.54, D/U ratio 2.10, whorls 4 5/8.

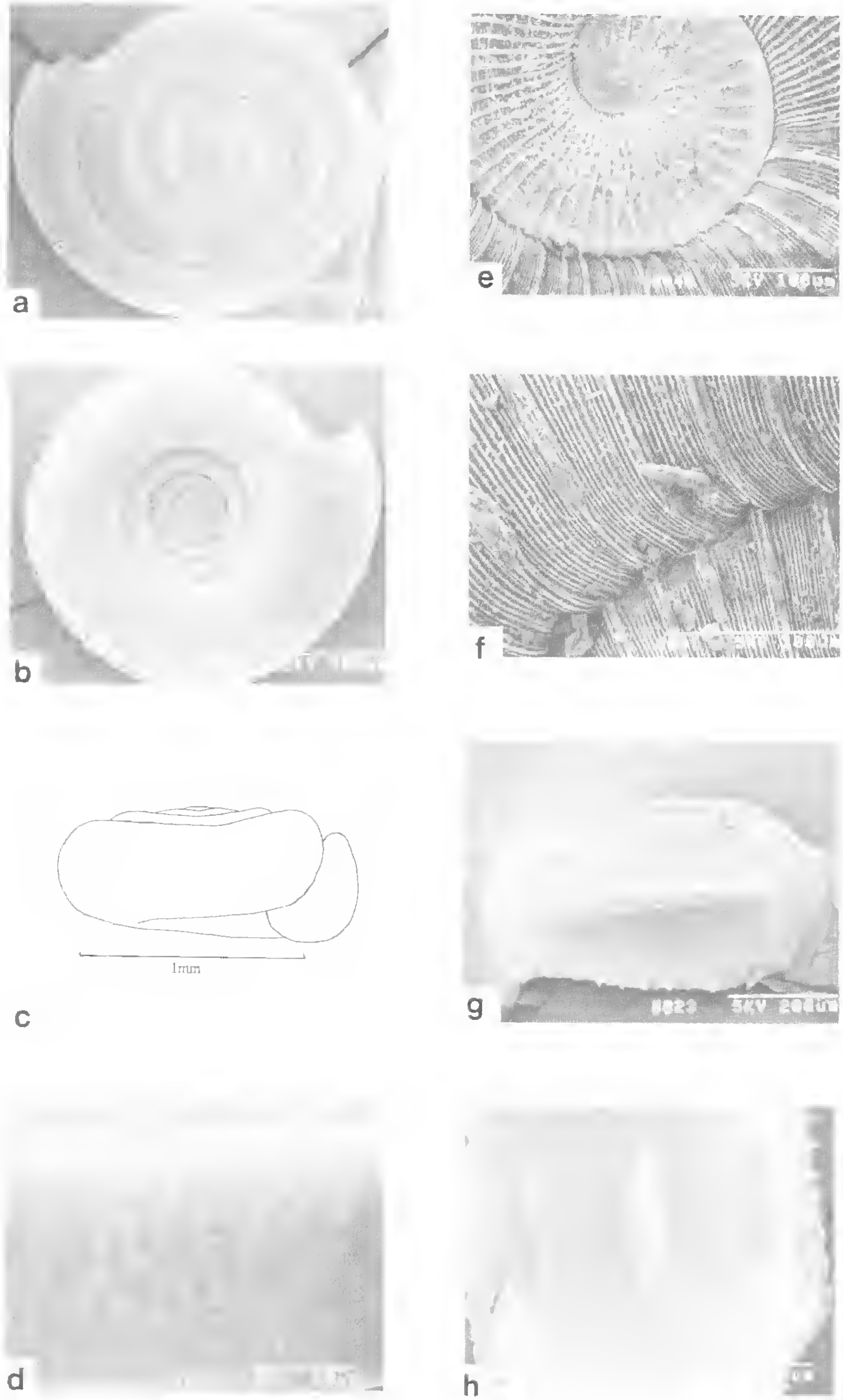
PARATYPES: QMMO12094, AMC136479, 29 specimens, same locality data as holotype; Bunya Mts N.P., SEQ, NVF (18 QMMO6089, 3 Mar 1976, M.J. Bishop); Dandabah, Bunya Mts N.P., SEQ, behind picnic area, (26°50'S, 151°37'E) (5, QMMO12280, AMC136604, 31 Aug 1982, AM/QM-ABRS); sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ (27°04'S, 152°41'E) NVF/*Araucaria* (3, QMMO-15078, 6 Sept 1983), J. Stanisic, D. Potter); Wratten's Camp, Wratten's S.F., SEQ (26°17'S, 152°20'E) NVF, litter (3, QMMO11554, 17 Jul 1980, J. Stanisic, A. Green); Little Yabba Creek, Imbil S.F., SEQ (26°28'S, 152°38'E), NVF (1, QMMO12023, 8 Sept 1982, AM/QM-ABRS); Fred's Rd, Mt Mee, SEQ (27°05'S, 152°43'E) rainforest, leaf litter (1, QMMO-17318, 14 Apr 1980, J. Stanisic, N. Hall, A. Green); Big Falls Circuit, Bunya Mts N.P., SEQ, SNVF, under logs (1, QMMO16852, 5 Nov 1985, J. Stanisic, D. Potter); Dandabah, Bunya Mts. N.P., SEQ (26°50'S, 151°35'E), NVF/*Araucaria* (16, QMMO6069, 5 Mar 1976, M.J. Bishop).

DIAGNOSIS

Shell minute, diameter 1.29–1.66 mm (mean 1.52 mm) with 4 3/8 to 4 5/8 (mean 4 1/2+) tightly coiled whorls. Last whorl descending more rapidly. Early spire and apex (Fig. 84a) flat to very slightly elevated, SP/BWW ratio 0.07–0.12 mm (mean 0.09 mm), height 0.64–0.76 mm (mean 0.70 mm). HD ratio 0.40–0.54 mm (mean 0.46 mm). Protoconch of 1 5/8 to 1 3/4 whorls, exsert, mean diameter 391.9 μm at 1 1/2 whorls. Apical sculpture (Fig. 84e) of curved radial ribs and spiral wrinkles. Post nuclear sculpture (Fig. 84f) of numerous, prominent, protractively sinuated radial ribs, 56–98 (mean 76.6 mm) ribs on the body whorl. Ribs/mm 10.98–21.26 mm (mean 16.23 mm). Microsculpture (Fig. 84f) of fine radial riblets, 8–12 between each pair of major ribs, and very low, barely visible, spiral cords which are raised at their junction with the microradials to produce a beaded effect. Umbilicus (Fig. 84b) wide, cup-shaped, diameter 0.60–0.72 mm (mean 0.65 mm). D/U ratio 2.09–2.59 mm (mean 2.35 mm). Sutures impressed, whorls rounded below and shouldered above a slightly, laterally compressed periphery (Fig. 84c). Aperture ovately lunate. Barriers present, consisting of three palatal and three parietal

TABLE 17 - LOCAL VARIATION IN *RHOPHODON MINUTISSIMUS* SP. NOV., *RHOPHODON COLMANI* SP. NOV. AND *RHOPHODON BAIRNSDALENSIS* (GABRIEL, 1930)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Rhophodon minutissimus												
Lacey's Creek												
OMMO 17316 (Holotype)	1	4 5/8	0.71l	1.29	0.54	0.04	0.53	0.08	78	19.17	0.62	2.10
OMMO 12094	2	4 5/8+	0.72±0.020 (0.70–0.74)	1.49±0.010 (1.48–1.50)	0.48±0.010 (0.47–0.49)	0.05±0.010 (0.04–0.06)	0.52±0.010 (0.51–0.53)	0.10±0.020 (0.08–0.12)	89.5±8.50 (81–98)	19.11±1.680 (17.43–20.79)	0.62	2.42±0.015 (2.40–2.43)
Mt Mee												
QMMO 15078	1	4 5/8	0.64	1.60	0.40	0.00	0.55	--	88	17.47	0.72	2.23
Wrattens S.F.												
OMMO 11554	1	4 3/8+	0.68	1.38	0.49	0.04	0.51	0.08	92	21.26	0.66	2.09
Bunya Mountains												
QMMO 6089	5	4 1/2- (4 3/8–4 5/8)	0.70±0.015 (0.68–0.76)	1.55±0.039 (1.46–1.66)	0.45±0.010 (0.42–0.48)	0.03±0.012 (0.04–0.06)	0.53±0.011 (0.49–0.55)	0.09±0.015 (0.07–0.12)	67.4±4.98 (56–80)	13.92±1.323 (10.98–17.21)	0.64±0.011 (0.60–0.66)	2.44±0.058 (2.29–2.59)
OMMO 12280	2 0	4 3/8+ (4 3/8+to4 1/2+)	0.70±0.020 (0.68–0.72)	1.59±0.010 (1.58–1.60)	0.44±0.015 (0.4–0.45)	0.05±0.010 (0.04–0.06)	0.53	0.10±0.020 (0.08–0.12)	72.5±0.50 (72–73)	14.49±0.195 (14.29–14.68)	0.67±0.030 (0.64–0.70)	2.39±0.090 (2.30–2.48)
Rhophodon colmani												
Kenilworth S.F.												
OMMO 17314 (Holotype)	1	4 5/8	0.64	1.56	0.41	0.04	0.47	0.09	28	5.70	0.66	2.38
OMMO 6288	4	4 1/2-	0.60±0.027 (0.53–0.66)	1.42±0.037 (1.34–1.52)	0.42±0.017 (0.38–0.46)	0.05±0.006 (0.04–0.06)	0.46±0.010 (0.43–0.47)	0.12±0.012 (0.09–0.14)	26.0±).29 (23–29)	5.83±0.23 (5.48–6.51)	0.56±0.020 (0.51–0.60)	2.54±0.037 (2.43–2.60)
Rhophodon bairnsdalensis												
Bairnsdale												
NMVF 704 (Holotype)	1	4 7/8	0.86	1.89	0.46	0.08	0.60	0.14	27	4.55	0.80	2.36
NMVF 30749	1	4 3/4	0.86	1.85	0.47	0.06	0.60	0.10	40	6.88	0.76	2.43
NMVF 53365	3	4 7/8 (4 3/4–5)	0.88±0.044 (0.80–0.95)	1.94±0.007 (1.93–1.95)	0.45±0.018 (0.42–0.48)	0.04±0.012 (0.02–0.06)	0.64±0.023 (0.60–0.68)	0.06±0.018 (0.03–0.09)	30.7±0.577 (29–331	5.02±0.184 (4.78–5.38)	0.06±0.018 (0.03–0.09)	2.41±0.083 (2.29–2.57)
Jemmy's Point												
NMVF 23326	1	4 5/8	0.76	1.95	0.39	---	0.62	---	30	4.89	0.80	2.44
SAMD 5683	2	4 7/8 (4 3/4–5-)	0.86±0.020 (0.84–0.88)	1.95	0.44±0.010 (0.43–0.45)	0.04±0.020 (0.02–0.06)	0.63±0.010 (0.62–0.64)	0.07±0.035 (0.03–0.10)	27.5±0.500 (27–28)	4.48±0.080 (4.40–4.56)	0.76±0.020 (0.74–0.78)	2.57±0.070 (2.50–2.64)
Lakes Entrance												
AMC 153706	1	(4 3/4–to 5 1/4)	0.83±0.035 (0.78–0.90)	1.95±0.084 (1.85–2.12)	0.43±0.003 (01.42–0.43)	0.04	0.63±0.013 (0.62–0.66)	0.06	26.7±2.33 (23–31)	4.33±0.203 (3.96–4.66)	0.80±0.031 (0.74–0.84)	2.44±0.068 (2.30–2.51)
AMC 103564	1	4 3/4	0.86	1.91	0.45	0.04	0.60	0.07	33	5.49	0.78	2.45
Braidwood												
AMC 126761	10	5 1/8- (4 7/8–5 3/8+)	0.88±0.018 (0.82–0.97)	2.15±0.044 (2.01–2.42)	0.41±0.003 (0.39–0.42)	0.07±0.013 (0.00–0.14)	0.64±0.006 (0.60–0.66)	0.11±0.022 (0.00–0.23)	39.7±2.61 (28–57)	5.86±0.349 (4.34–8.33)	1.01±0.023 (0.92–1.13)	2.14±0.024 (2.02–2.24)
Yarrangobilly Caves												
AMC 142959	10	5- (4 3/4–5 1/8+)	0.96±0.021 (0.86–1.05)	2.12±0.028 (2.01–2.30)	0.45±0.008 (0.42–0.48)	0.07±0.007 (0.04–0.10)	0.66±0.008 (0.64–0.72)	0.10±0.011 (0.06–0.16)	40.4±1.32 (35–47)	6.06±0.207 (4.98–7.00)	0.85±0.016 (0.78–0.97)	2.51±0.024 (2.38–2.66)


a
b
c
1mm
d
e
f
g
h

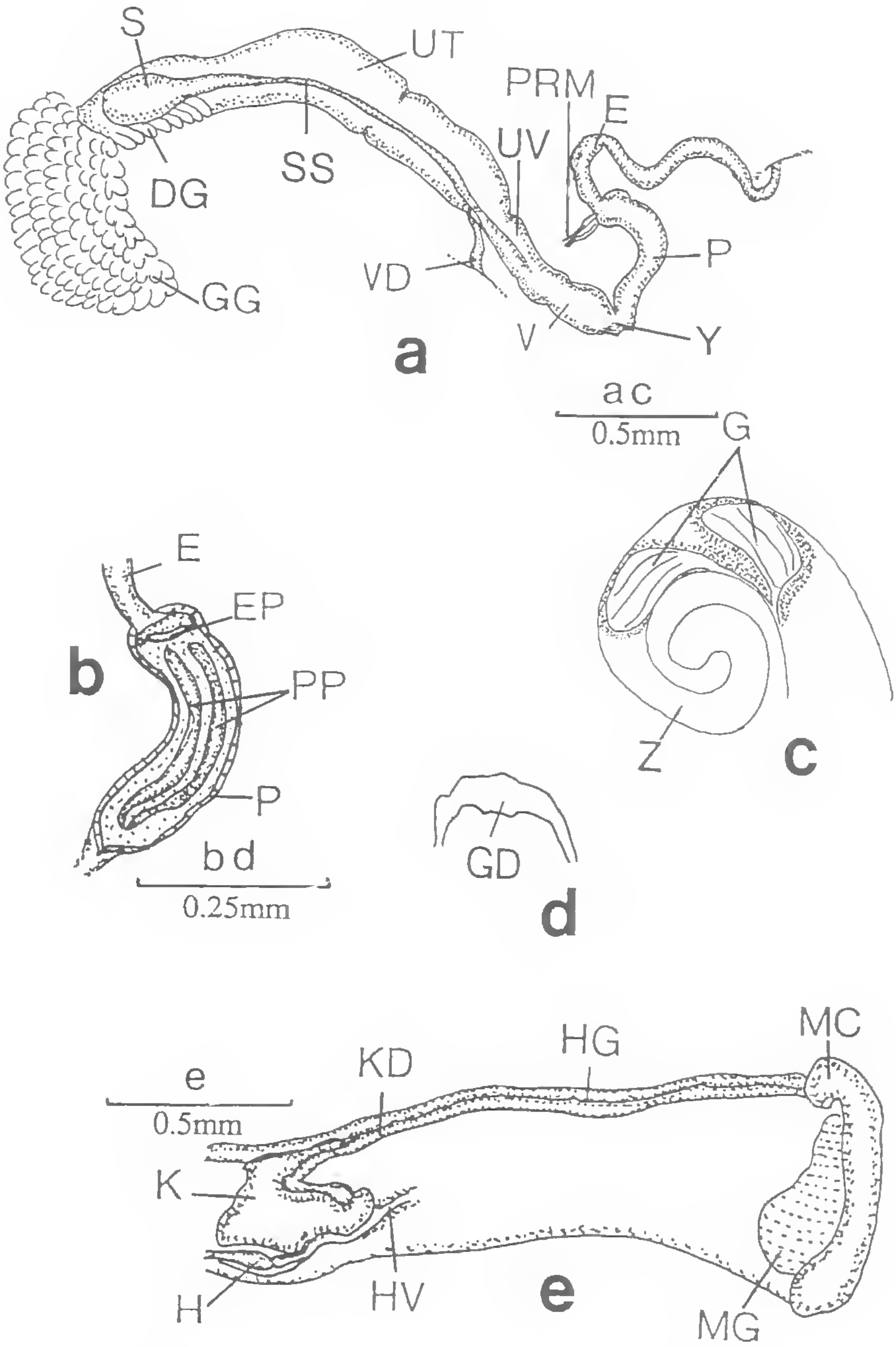


FIG. 85. *Rhophodon minutissimus* sp. nov. Big Falls Circuit, Bunya Mts N.P., SEQ. QMMO16852, paratype. a, genitalia; b, penis interior; c, ovotestis; d, hermaphroditic duct; e, pallial cavity. Scale lines as marked.

FIG. 84. *Rhophodon minutissimus* sp. nov. a–h, c. 1km S of Raynbird Creek Rd, on Lacey's Creek Rd, Lacey's Ck, SEQ. QMMO12094, paratype. a–c, entire shell; d, microdenticulations on surface of upper parietal; e, apical sculpture; f, post nuclear sculpture; g, parietal barriers; h, palatal barriers. Scale lines as marked.

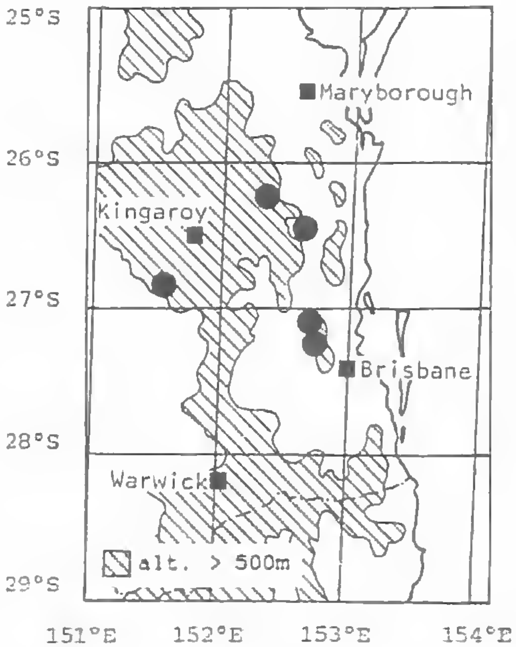


FIG. 86. Distribution of *Rhophodon minutissimus* sp. nov.

lamellae (Fig. 84g). First and third parietal lamellae large with anterior edge protruding from aperture. expanding posteriorly; second deeply recessed, short, crescent-shaped. All directed downwards. Palatal lamellae (Fig. 84h) deeply recessed, short, crescentic. Lip simple without columella expansion or reflection. Parietal callus developed. Colour golden-brown. Based on 12 measured adults.

Genitalia with epiphallus (Fig. 85a) thick, coiled, muscular; longer than the penis, internally with longitudinal pilasters, entering the penis apically through two fleshy thickenings (Fig. 85b). Penial retractor muscle inserted at the penis/epiphallus junction. Penis a broad muscular tube with sheath; internally with longitudinal fleshy pilasters (Fig. 85b).

Radula typical.

Based on 2 dissected adults (QMMO16852).

RANGE AND HABITAT

Notophyll vine forests of the D'Aguilar Range, Bunya Mountains, and the Coast Range near Gympie, SEQ. *R. minutissimus* has been collected in litter and from under logs.

REMARKS

Ability to exist in drier open forest is probably a contributing factor to the comparatively wide distribution of this species. *R. bairnsdalensis* displays similar adaptability and breadth of distribution.

Rhophodon colmani sp. nov.
(Figs 87–88; Tables 15, 17)

ETYMOLOGY

For Mr Phillip Colman, Australian Museum.

COMPARISONS

Small size, almost flat spire, widely spaced ribs, open umbilicus and apertural barriers, effectively separate *R. colmani* from any sympatric charopid. *Egilomen cochlidium* from the McPherson Ranges is grossly similar in shell form, but lacks apertural barriers, and has a larger shell with higher whorl count, higher rib count and more elevated spire.

Conchologically *R. colmani* is most similar to *R. bairnsdalensis* from southern NSW and Victoria. However the latter species is larger, with more ribs, wider umbilicus, greater number of whorls and quite different pattern of apertural barriers. The three parietal, six palatal and single columellar barrier of *R. colmani* (Fig. 87f-h) contrast with the single parietal and two palatals of *R. bairnsdalensis* (Fig. 90a-c).

TYPE MATERIAL

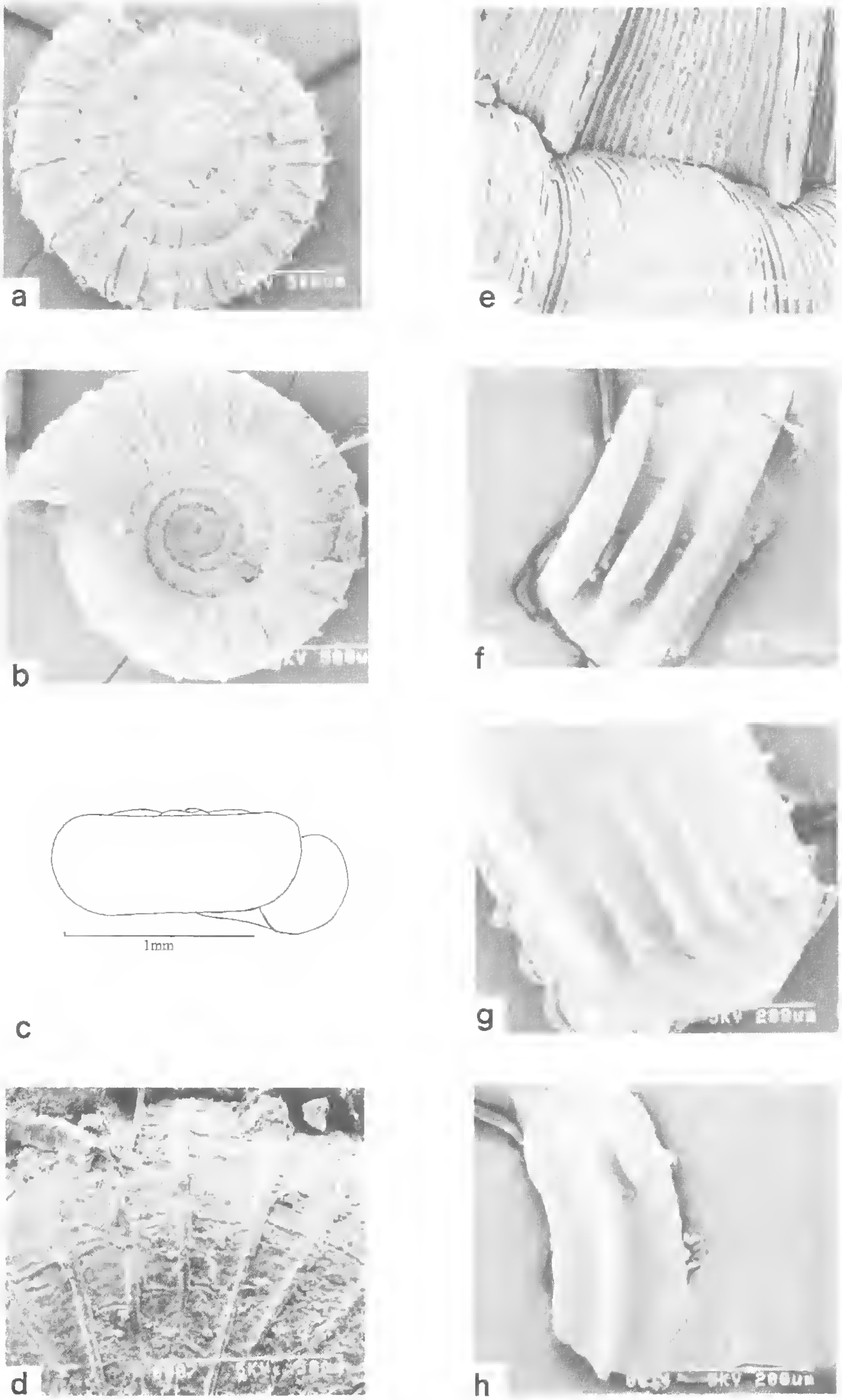
HOLOTYPE: QMMO17314, Kenilworth State Forest, SEQ (26°35'S, 152°36'E) mixed notophyll vine forest. Collected by M.J. Bishop, 18 May 1976. Height of shell 0.64 mm., diameter 1.56 mm, H/D ratio 0.41, D/U ratio 2.38, whorls 4 5/8.

PARATYPES: QMMO6288, 14 specimens, same collection data as holotype.

DIAGNOSIS

Shell minute, diameter 1.34–1.56 mm (mean 1.45 mm) with 4 1/4 to 4 5/8 (mean 4 1/4-) tightly coiled whorls, the last descending more rapidly. Early spire and apex (Fig. 87a) flat to very slightly elevated. SP/BWW ratio 0.09–0.14 mm (mean 0.11 mm), height 0.53–0.66 mm (mean

FIG. 87. *Rhophodon colmani* sp. nov. Kenilworth S.F., SEQ. QMMO6288, paratypes. a-c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, parietal barriers; g, palatal barriers; h, columellar barrier. Scale lines as marked.


a
e
b
f
1mm
c
g
d
h

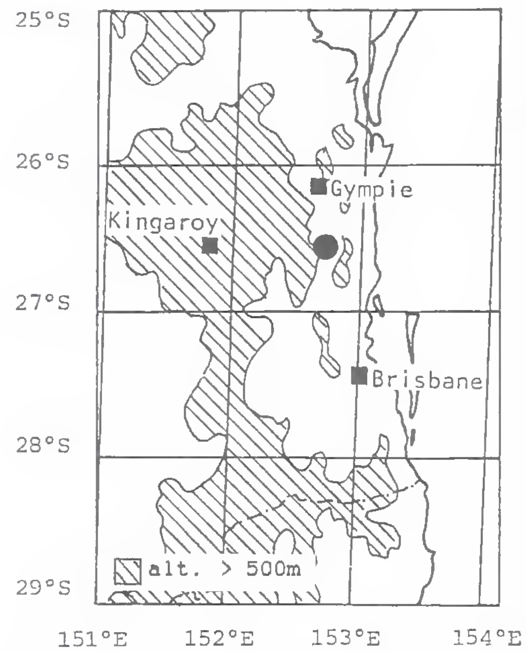


FIG. 88. Distribution of *Rhophodon colmani* sp. nov.

0.61 mm). H/D ratio 0.38–0.46 mm (mean 0.42 mm). Protoconch of 1 1/2 to 1 5/8 whorls, exsert, mean diameter 357.4 µm at 1 1/2 whorls. Apical sculpture (Fig. 87d) of curved radial ribs, becoming more numerous at the nuclear-postnuclear junction, and fine almost obsolete spiral threads and wrinkles. Postnuclear sculpture (Fig. 87e) of bold, widely spaced, protractively sinuated radial ribs, 23–29 (mean 26.4) ribs on the body whorl. Ribs/mm 5.48–6.51 (mean 5.81). Microsculpture (Fig. 87e) of fine radial riblets, 17–25 between each air of major ribs, and low spiral cords. Umbilicus (Fig. 87b) wide, cup-shaped, diameter 0.51–0.66 mm (mean 0.58 mm). D/U ratio 2.38–2.60 mm (mean 2.50 mm). Sutures impressed. Whorls rounded below and strongly shouldered above a compressed periphery (Fig. 87e). Aperture ovately lunate. Barriers numerous consisting of three large parietal barriers (Fig. 87f) protruding from the aperture, a large columellar barrier (Fig. 87h) situated inside the aperture margin, and six palatal barriers (Fig. 87g) set back about 1/8 whorl. First palatal barrier small, crescent-shaped, tapering rapidly anteriorly; second similar in shape, but with longer taper anteriorly; third and fourth about twice the size of the second with long anterior tapers; fifth almost equal in size to the second, rapidly tapering anteriorly; sixth elongate, thread-like, about twice the length of the others. Columellar barrier (Fig. 87h) a large crescent-shaped lamella situated well inside the aperture. First parietal barrier long expanded posteriorly and directed upward; second and third, thin anteriorly, expanding posteriorly, swollen. Lip simple, without columella expansion or deflection. Parietal callus well developed. Colour light straw-yellow. Based on 5 measured adults.

Anatomy unknown.

RANGE AND HABITAT

Notophyll vine forest of Kenilworth State Forest, SEQ. No data are available on microhabitat.

REMARKS

Lack of soft parts and poor distributional data restrict discussion. *R. colmani* is most likely sympatric with *R. minutissimus* and it is tempting to speculate that the sharply altered shell patterns, in particular the increased number of palatal barriers, represent character displacement under conditions of sympatry.

Rhophodon bairnsdalensis (Gabriel, 1930) comb. nov. (Figs 89–92; Tables 15, 17)

Charopa bairnsdalensis Gabriel, 1930, p. 78, pl. 2, figs 11-12.

Endodonta bairnsdalensis (Gabriel); Kershaw, 1956a, p. 137

Egilodonta bairnsdalensis (Gabriel); Iredale, 1937a, p. 329.

PREVIOUS STUDIES

Iredale (1937) included this species in a new genus *Egilodonta* based on the presence of apertural barriers. He did not give reasons for separating the species from the northern *Rhophodon* nor from the geographically more proximate *Dentherona* Iredale, 1933 and *Bischoffena* Iredale, 1937. While *R. bairnsdalensis* has fewer apertural lamellae than other species of *Rhophodon*, shell sculpture is comparable, as is the structure of the pallial cavity and terminal male genitalia. A review of *Dentherona* and *Bischoffena* is beyond the scope of this study, but coiling patterns and microsculptural details of these genera suggest that they are not related.

COMPARISONS

R. bairnsdalensis can be separated from its congeners by its average size, widely spaced

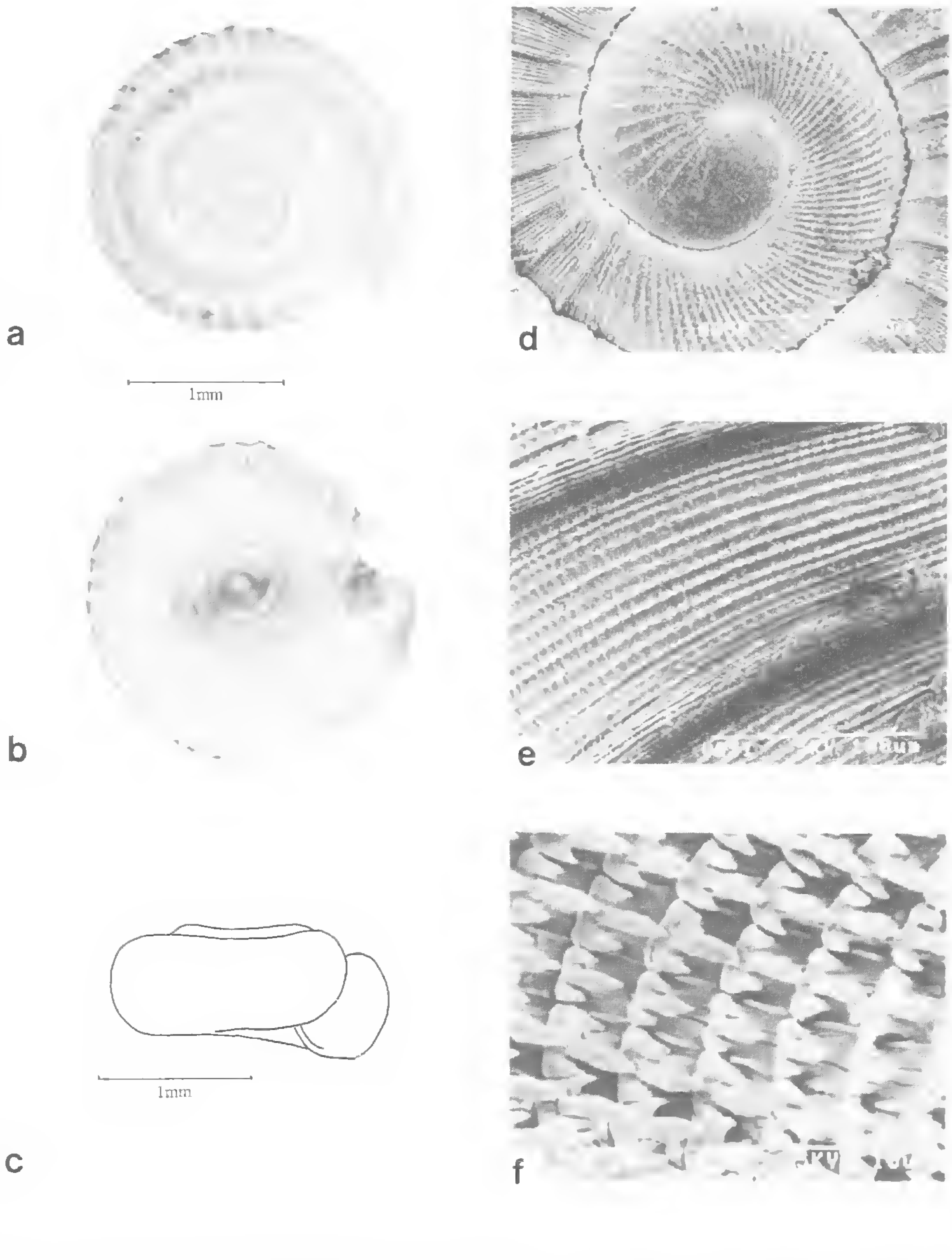


FIG. 89. *Rhophodon bairnsdalensis* (Gabriel, 1930). a–e, Marble Arch, S of Braidwood, NSW. AMC126761; f, near Lakes Entrance, VIC. NMVF53160. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, central and lateral teeth. Scale lines as marked.

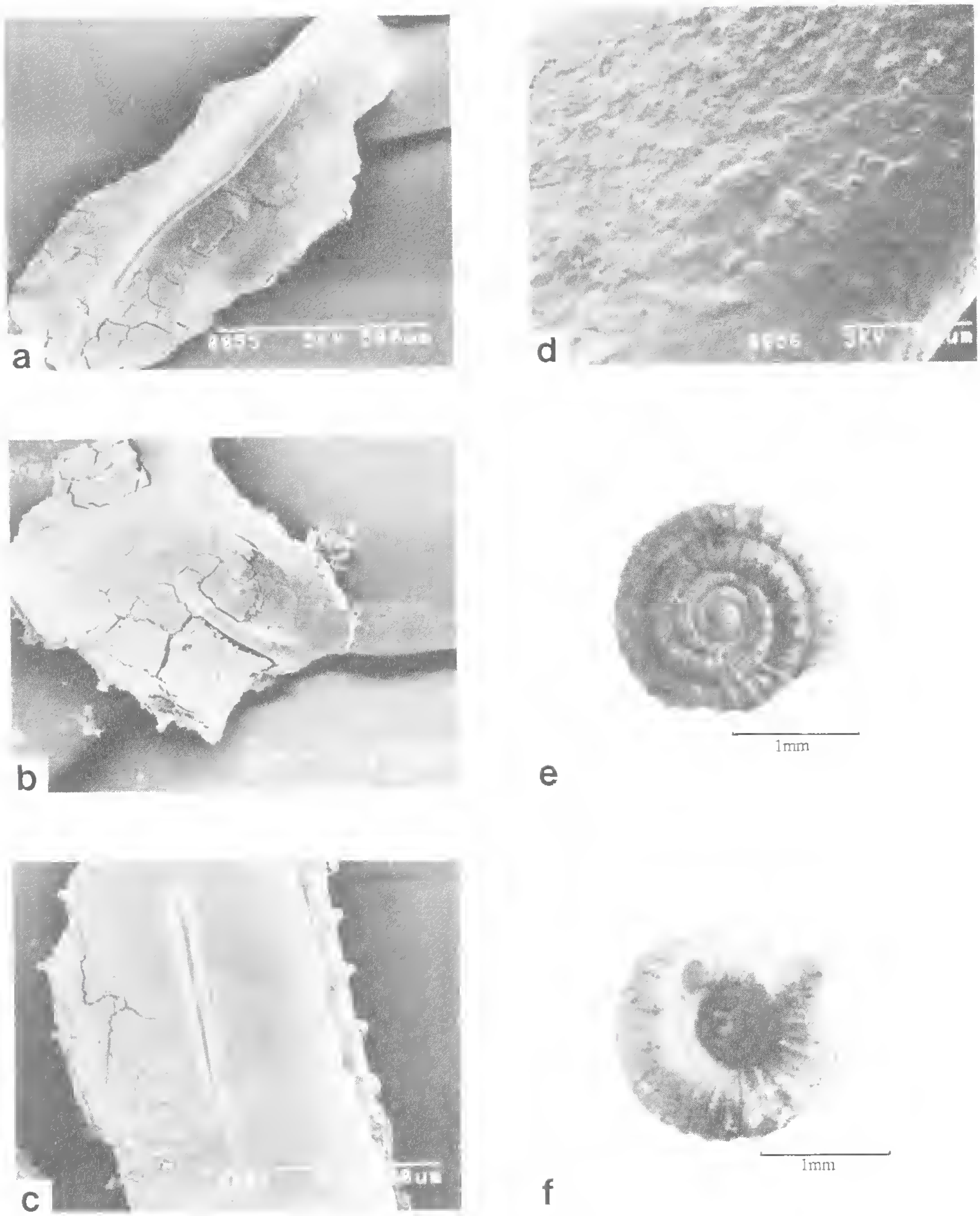


FIG. 90. *Rhophodon barinsdalensis* (Gabriel, 1930). a–d, Marble Arch, S of Braidwood, NSW. AMC126761; e–f, Bairnsdale, VIC. NMVF 704, holotype. a, parietal barrier; b, basal barrier; c, palatal barrier; d, surface of parietal barrier.

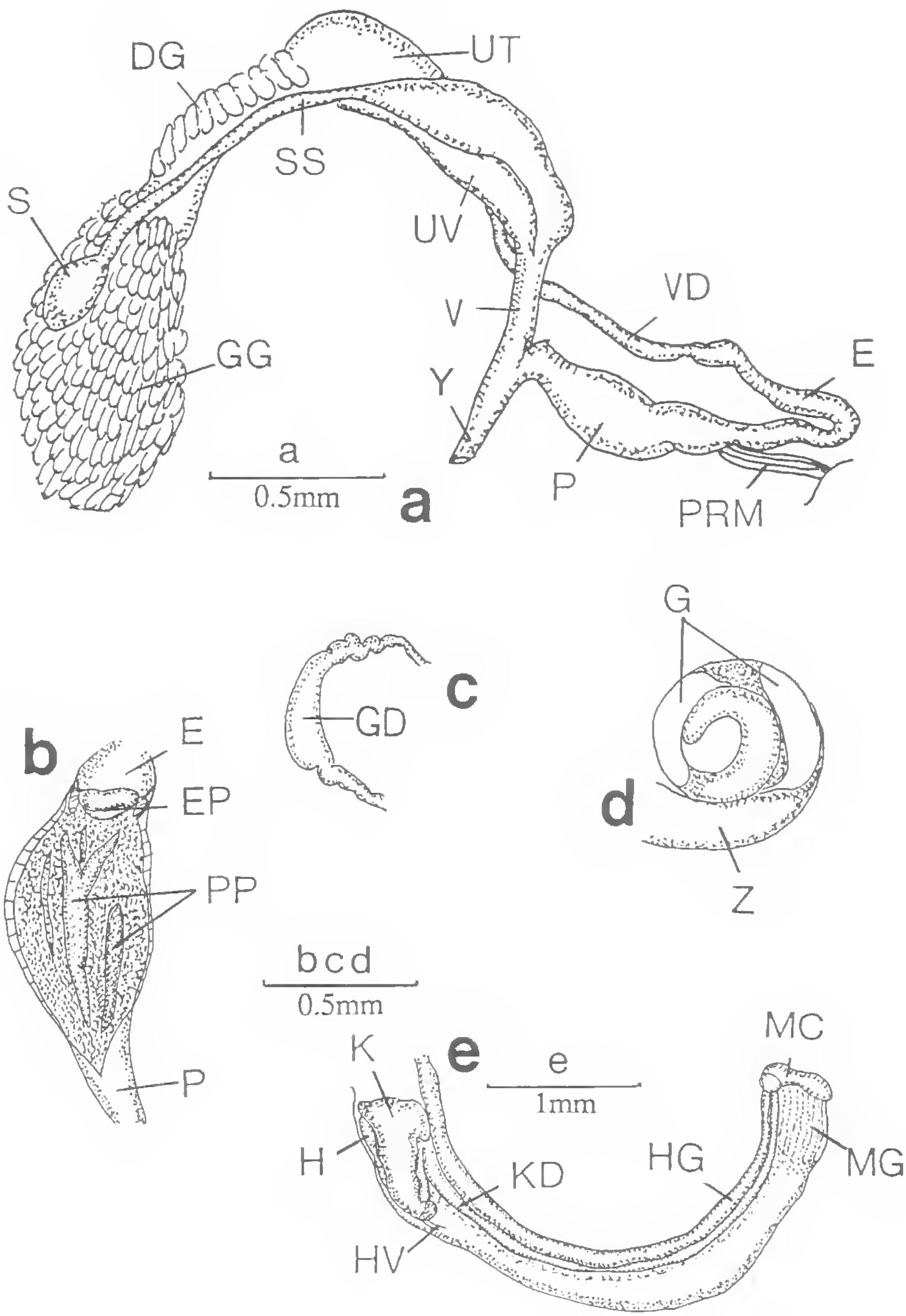


FIG. 91. *Rhophodon bairnsdalensis* (Gabriel, 1930). In leaf litter of damp forest gully, near Lakes Entrance, VIC. NMVF53160. a, genitalia; b, penis interior; c, d, ovotestis; e, talon and carrefour region; f, pallial cavity. Scale lines as marked.

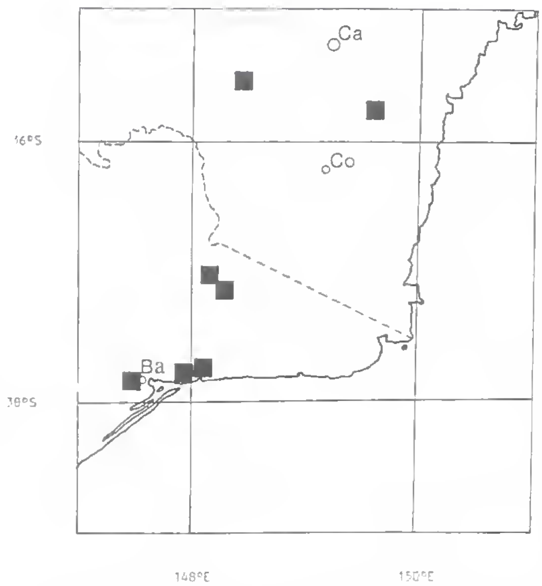


FIG. 92. Distribution of *Rhophodon bairnsdalensis* (Gabriel, 1930) in south-east New South Wales and Victoria. (Ca = Canberra; Co = Cooma; Ba = Bairnsdale).

radial ribs, wide umbilicus and only three apertural barriers (one parietal, two palatal) (Fig. 90a-c). *R. colmani* is smaller, with fewer widely spaced ribs, has a smaller umbilicus and nine apertural barriers. Other *Rhophodon* species have a much higher number of ribs on the body whorl and are more easily distinguished from *R. bairnsdalensis* (Table 15). *'Charopa' jemmysensis* Gabriel, 1947, *'Charopa' colliveri* Gabriel, 1947 and *'Charopa' snowyensis* Gabriel and McPherson, 1947 are all sympatric with *R. bairnsdalensis* and have bold radial sculpture on the postnuclear whorls. However these species lack apertural barriers.

Type Material

Holotype: NMVF704, Bairnsdale, Victoria. Collected by T. Worcester. Height of shell 0.86 mm, diameter 1.89 mm, H/D ratio 0.46, D/U ratio 2.36, whorls 4 7/8.

Paratypes: NMVF30749, 2 specimens, same data as holotype.

Other Material

Jemmy's Point, Lakes Entrance, VIC, (5, NMVF-25277, C.J. Gabriel; 6, NMVF23326; 7, SAMD5683, Jan 1936, C.J. Gabriel; 7, SAMD5683 C.J. Gabriel); Wombargo Creek, VIC, rock bank above 3000 ft (1, NMVF1678); Toorloo Scenic Reserve, Toorloo Arm, 9m E of Lakes Entrance, VIC, damp forest gully, leaf litter (40, NMVF53367, 6 Dec 1970, D.C. Long); near Mitchell River, 2m from Bairnsdale, VIC (5, NMVF-53365, C. Oke); Jemmy's Point, Kalimna, VIC, leaf litter at foot of cliff (6, NMVF53366, 7 Dec 1970, D.C. Long); in leaf litter of damp forest gully, near Lakes Entrance, VIC (7, NMVF53160); Toorloo Arm, Princes Hwy, 6 mls N of Lakes Entrance, VIC (7, AMC153706, 6 Nov 1963, L. Price); Bridle Creek, c. 0.5km N of Ballantyne's Gap, Buchan-Jindabyne Rd, VIC under leaves and logs of damp gully in gum forest (31, AMC153704, AMC154810, 13 Jan 1980, W.F. Ponder, P.H. Colman); Lakes Entrance, VIC (1, AMC103564, Jan 1935, C.J. Gabriel); Marble Arch, S of Braidwood, NSW (35°44'S, 149°41'E), in litter in deep gully on limestone (180, AMC126761, 17 Jan 1981, W.F. and W.F. Ponder); Yarrangobilly Caves, NSW, beside trail to river cave, in litter (144, AMC142959, 31 Oct 1980, W.F. Ponder, J. Hall); 4 mls E of Lake Tryon turnoff on main road, near Lakes Entrance, VIC, in dense bush under leaves and logs on ground (64, AMC154770, 10 Jan 1970, W.F. Ponder, P.H. Colman); Leather Barrel Creek, near Murray River, Alpine Way, Kosciusko N.P., NSW, in open forest with some scrub, in leaf litter (19, AMC154808, 1970, W.F. Ponder, P.H. Colman); Deep Creek, Kiewa Hwy, c. 5 ml N of Tawonga, VIC, in open bush on roadside, leaf litter (20, AMC154757, 18 Jan 1970, W.F. Ponder, P.H. Colman); Mt Drummer, VIC (21, AMC154728, 27 Sept 1959, D.F. McMichael).

Diagnosis

Shell minute, diameter 1.85–2.42 mm (mean 2.06 mm), with 4 5/8 to 5 3/8+ (mean 5) tightly coiled whorls. Apex and early spire (Fig. 89a) depressed, flat or only slightly elevated, SP/BWW ratio 0.00–0.23 (mean 0.10), height 0.76–1.05 mm (mean 0.89 mm). HD ratio 0.39–0.48 mm (mean 0.43 mm). Protoconch of 1 1/2 to 1 5/8 whorls, exsert, mean diameter 385.8 µm at 1 1/2 whorls. Apical sculpture (Fig. 89d) of curved radial ribs, more crowded at the nuclear-postnuclear junction, and fine spiral threads. Post nuclear sculpture (Fig. 89e) of bold, widely spaced, slightly protractively sinuated radial ribs, 23–57 (mean 36.2) ribs on the body whorl. Ribs/mm 3.96–8.33 (mean 5.56). Microsculpture (Fig. 89e) of fine radial riblets, 10–22 between each pair of major ribs, and fine microspiral cords which are continuous on the apices of the radial ribs, and raised at their junction with the microradials to produce a beaded effect. Umbilicus (Fig. 89b) wide, cup-shaped, diameter 0.74–1.13 mm (mean 0.88 mm), D/U ratio 2.02–2.66 (mean 2.37). Sutures impressed.

Whorls rounded below and shouldered above a compressed periphery (Fig. 89c). Aperture ovately lunate. Three apertural barriers present. Parietal barrier (Fig. 90a), low, elongate, thread-like anteriorly, protruding beyond the lip margin, expanded and deflected downwards posteriorly. Parietal trace sometimes present. Palatal barriers two. First (Fig. 90b), short, low, crescent-shaped situated at the baso-columellar margin; second (Fig. 90c) elongate, slender, located halfway up margin of outer lip. Lip simple with no columellar thickening or deflection. Parietal callus present. Colour golden yellow-horn to white with light-brown radial suffusions. Based on 32 measured adults.

Genitalia with epiphallus/vas deferens junction valvular. Epiphallus (Fig. 91a) reflexing and looping the penial retractor muscle before entering the penis apically through a simple pore (Fig. 91b) flanked by two fleshy thickenings, internally with longitudinal pilasters. Penial retractor muscle inserting at the epiphallus/penis juntion. Penis (Fig. 91b) with apical bulb. Main penial chamber interior with a fleshy longitudinal pilaster and several low longitudinal thickenings (Fig. 91b).

Radula (Fig. 89f) typical.

Based on three dissected adults (NMV-F53160).

RANGE AND HABITAT

From Bairnsdale, Victoria, north through the Snowy Mountains area to the Yarrangobilly Caves and Braidwood, southern NSW. The species lives in open scrub, moist forest and on limestone outcrops. Microhabitat appears to be in litter and under logs.

REMARKS

R. bairnsdalensis is a southern outlier separated from its nearest relative, *R. kempseyensis*, by almost 500 km.

Discocharopa Iredale 1913

Discocharopa Iredale, 1913, pp. 279–280; Iredale, 1937a, p. 325; Kershaw, 1956a, p. 140; Burch, 1976, p. 132; Solem, 1983, p. 74; Solem, 1984, p. 164.

TYPE SPECIES

Charopa, (*Discocharopa*) *exquisita* Iredale, 1913; by original designation.

REMARKS

For diagnosis see Solem (1983, p. 74). Solem (1983, p. 76) gives a full synonymy of a range of geographic variations.

Discocharopa aperta (Möllendorff, 1888)
(Figs 93–94; Tables 15, 18)

Patula aperta Möllendorff, 1888, p. 89

Endodonta concinna Hedley, 1901, p. 279, pl. 48, figs 1–3.

Discocharopa concinna (Hedley); Iredale, 1937a, p. 325.

Discocharopa aperta (Möllendorff); Solem, 1983, pp. 76–81, figs 35–37; Solem, 1984, pp. 164–165, figs 9–10, 22–27.

PREVIOUS STUDIES

Solem (1983) synonymised *D. concinna* with *D. aperta*, *D. planorbulina* (Tate, 1896) from Central Australia, and further species from Indonesia, New Hebrides, Fiji, Kermadecs, Samoa and the Society Islands. In spite of differences in apertural barriers, intensity of spiral sculpture, size, umbilical width and rib count. Solem (1983) could not effectively separate the distant populations and opted for a single wide ranging species. Solem (1984) reviewed the Australian distribution of this species and provided records from west, north-west and central Australia with brief mention of likely distribution limits in eastern Australia. In the absence of soft parts for study, Solem's classification is maintained, although it is probable that the SEQ populations may be a separate species derived from local charopid ancestors.

COMPARISONS

D. aperta is distinguished by its minute, white shell which has normally coiled whorls, almost flat spire, crowded, protractively sinuated radial ribs, and wide saucer-shaped umbilicus (Fig. 93). *D. aperta* bears a general similarity to *Rhophodon* in apical sculpture, and in particular with *R. kempseyensis* in microsculpture on postnuclear whorls. However, *Rhophodon* has more shouldered, tightly coiled whorls, a cup-shaped umbilicus and few to many apertural barriers. Solem (1983), using material from the Kermadec Islands, showed the species to have terminal male genitalia without an externally differentiated epiphallus. While *Cralopa* Iredale, 1941 approaches this condition, the lack of an epiphallus is more prevalent among New Zealand charopids.

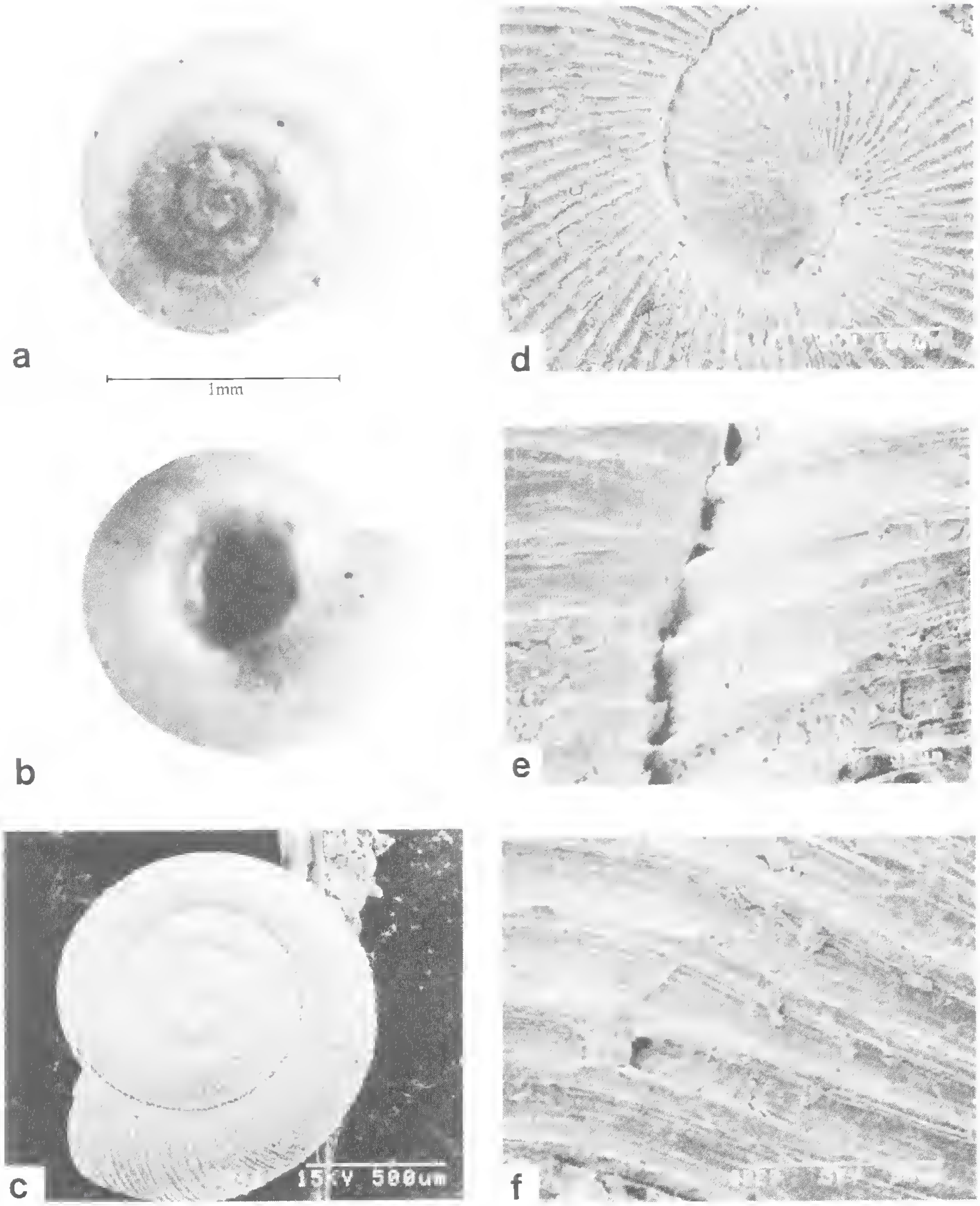


FIG. 93. *Discocharopa aperta* (Möllendorff, 1888). a–b, Bundaberg, Qld. AMC8970, lectotype; c–f, c. 1.8km E of Builyan Rwy Station, on Builyan-Gladstone Rd, SEQ. QMMO17308. a–c, entire shell; d, apical sculpture; e–f, post nuclear sculpture. Scale lines as marked.

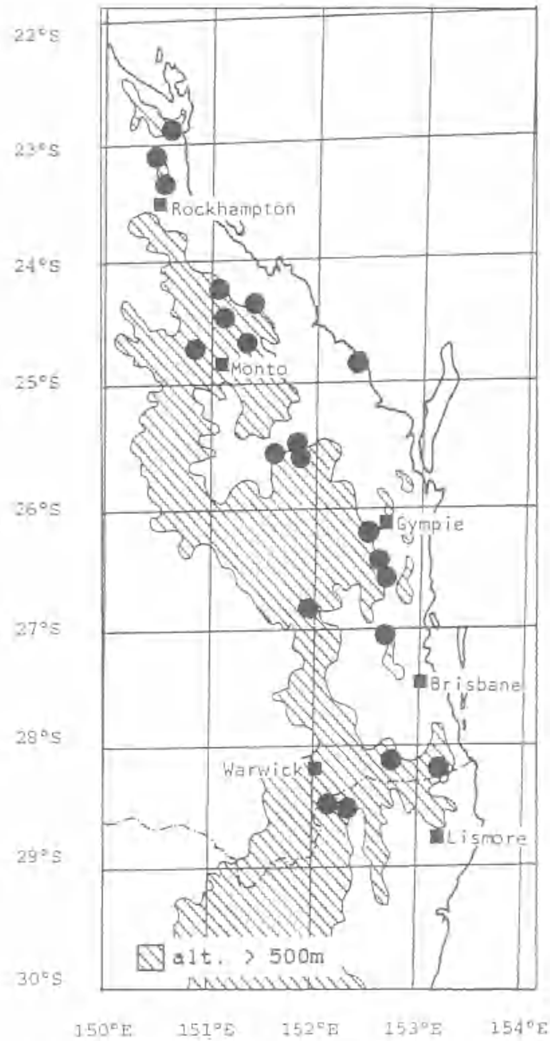


FIG. 94. Distribution of *Discocharopa aperta* (Möllendorff, 1888) in southeast Queensland.

TYPE MATERIAL

LECTOTYPE (designated Solem, 1983, p. 77): AMC-8970, Bundaberg, Qld., ex May. Height 0.61 mm, diameter 1.48 mm, H/D ratio 0.45, D/U ratio 2.81, whorls 31/2.

PARALECTOTYPES: AMC63489, 7 specimens, same data as lectotype.

OTHER MATERIAL

c. 1 km from Olsen's Caves, MEQ (23°10'S, 150°30'S) litter, limestone outcrop (16, QMMO-17307, 13 Jul 1980, J.Stanisic, A. Green, G. Annabell); Mt Archer, Bersaker Ra.,MEQ (23°21'S, 150°35'E), remnant vine thicket (6, QMMO11922, 30 Jun 1982, J. Stanisic); c. 2 km W of Gayndah, on Gayndah-Hinesville Rd, SEQ (25°38'S, 151°36'E) bottle tree scrub/SEVT, under rocks and in litter (2, QMMO11528,16 Jul 1980, J. Stanisic, A. Green); Dan Dan Scrub, SEQ, SEVT, in litter (2, QMMO16800, 10 May 1984, J. Stanisic, D. Potter); Dawes Range, SEQ (24°28'S, 151°07'E) MVF/*Araucaria* (28, QMMO12666, AMC136795, 4 Sept 1982, AM/QM - ABRS); c. 1.8 km E of Builyan Rwy Stn, on Builyan-Gladstone Rd, SEQ (24°22'S, 151°24'E), rainforest on river bank litter (13, QMMO17308, 15 Jul 1980, J. Stanisic, A. Green); Mt Biggenden, SEQ (25°32'S, 151°50'E), SEVT, limestone outcrop (5, QM-MO17309, 8 Jul 1980, J. Stanisic, A. Green; 1, QM-MO16838, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton; 14, QMMO11958, AMC136396, 3 Sept 1982, AM/QM - ABRS); Walla Range, E of Ban Ban Springs, SEQ (25°38'S, 151°50'E) SEVT (1, QMMO-12414, 3 Sept 1982, AM/QM - ABRS); Kalpowar S.F., SEQ MVF/*Araucaria* (2, QMMO17310, 15 Jul 1980, J. Stanisic, A.Green; 2, QMMO17306, 4 Sept 1982, AM/QM - ABRS); Gavial Ck, Bouldercombe, MEQ (23°34'S, 150°28'E) MVF, litter (4, QMMO-16808, 9 Jul 1983, J. Stanisic, D. Potter); Coalstoun Lakes Rd, Coalstoun Lakes, SEQ (25°37'S, 151°53'E) SEVT (1, QMMO12396, 2 Sept 1982, AM/QM - ABRS); c. 54 km S of Biloela, on Biloela-Monto Rd, SEQ (24°45'S, 150°50'E) SEVT on rocky outcrop, litter (3, QMMO17311, 14 Jul 1980, J. Stanisic, A. Green); Mt Etna, MEQ (23°09'S, 150°27'E) MVF on limestone outcrop, litter (100, QMMO17312, 13 Jul 1980, J. Stanisic, A. Green, G. Annabell); Johannsen's Caves, MEQ (23°09'S, 150°27'E) MVF on limestone outcrop, litter (19, QMMO17313, 13 Jul 1980, J. Stanisic, A. Green, G. Annabell); Cammoo Caves, c. 24 km N of Rockhampton, MEQ (23°10'S, 150°27'E) limestone outcrop (4,AMC152145, W. Ponder, P.H. Colman, J.B. Burch, 8 Sept, 1970); Glastonbury SF, c. 0.25 km S of forestry station (26°13'30"S, 152° 29' 45"E) (1, QMMO13305, 7 Sept 1982,AM/QM-ABRS); S of Gympie, entrance to state forest off Yabba Ck Road (26°28'S, 152°38'E) (3, AMC. 138110 QMMO13365, 7 Sept 1982, AM/QM-ABRS); Kenilworth SF, SEQ (26°37'S, 152°42'E), rainforest, leaf litter (6, QMMO8360, 22 May 1980, J. Stanisic, A.Green); sidetrack off Mt Archer Rd, Mt Mee SF, SEQ (27°04'S, 152°41'E) (1, QMMO12173, 31 Aug 1982, AM/QM-ABRS); Natural Bridge NP, SEQ (28°13'S, 153°14'E) NVF (4, QMMO10453, AMC129266, 18 Mar 1981, AM/QM-ABRS); Fred's Rd, Mt Mee, SEQ (27°05'S, 152°43'E) rainforest, litter (3, QMMO8357, 14 Apr 1980, J. Stanisic, N. Hall, A. Green); Yarraman Forest Drive, Yarraman SF, SEQ (26°50'S, 151°57'E) MVF (1, QMMO-12261, AMC136586, 31 Aug 1982, AM/QM-ABRS

TABLE 18 - LOCAL VARIATION IN *DISCOCHAROPA APERTA* (MOLLENDORFF, 1888) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	Q/U RATIO
Discocharopa aperta												
Bundaberg OMMO 8970 (Lectotype *concinna*)	1	3 5/8	0.65	1.46	0.45	0.13	0.40	0.13	102	26.55	0.60	2.43
Mt Biggenden QMMO 17309	1	3 5/8+	0.53	1.21	0.44	0.04	0.33	0.12	110	34.55	0.48	2.52
Builyan QMMO 17308	4	3 3/8 (3 1/4–3 3/4-)	0.48±0.032 (0.42–0.57)	1.14±0.044 (1.03–1.23)	0.42±0.025 (0.35–0.46)	0.04±0.012 (0.02–0.07)	0.30±0.011 (0.28–0.33)	0.12±0.035 (0.07–0.22)	100.5±2.86 (93–108)	33.97±1.594 (29.70–36.52)	0.43±0.035 (0.36–0.51)	2.71±0.212 (2.41–3.31)
Kalpowar S.F. QMMQ 17306	2	3 1/4 (3 1/8–3 3/8)	0.57±0.070 (0.50–0.64)	1.18±0.010 (1.17–1.19)	0.49±0.065 (0.42–0.55)	0.05±0.010 (0.04–0.06)	0.36±0.025 (0.33–0.38)	0.14±0.020 (0.12–0.16)	95.5±2.13 (90–101)	32.31±3.57 (28.74–35.87)	0.49±0.045 (0.44–0.53)	2.46±0.245 (2.21–2.70)
Dawes Range QMMQ 12666	3	3 5/8 (3 5/8-to3 5/8)	0.53±0.015 (0.51–0.56)	1.20±0.024 (1.15–1.23)	0.45±0.023 (0.41–0.49)	0.03±0.007 (0.02–0.04)	0.33±0.007 (0.32–0.34)	0.08±0.023 (0.06–0.13)	106.3±1.43 (103–112)	33.77±0.715 (32.35–34.60)	0.47±0.026 (0.42–0.51)	2.56±0.923 (2.37–2.74)
Dan Qan Scrub QMMO 16800	1	3 3/4	0.52	1.27	0.41	0.03	0.34	0.09	...	...	0.53	2.40
Mt Archer QMMO 11922	1	3 3/4	0.58	1.23	0.47	0.05	0.33	0.16	116	35.84	0.52	2.37
Olsen's Caves QMMO 17307	4	3 5/8+ (3 5/8–3 3/4)	0.47±0.011 (0.44–0.49)	1.22±0.031 (1.15–1.29)	0.39±0.017 (0.35–0.42)	0.03	0.33±0.003 (0.32–0.33)	0.10±0.003 (0.09–0.10)	96.5±5.85 (82–110)	30.04±1.523 (26.18–33.44)	0.52±0.023 (0.48–0.57)	2.36±0.049 (2.26–2.48)
Gympie QMMO 13305	1	3 1/4	0.45	1.03	0.45	0.04	0.29	0.14	95	35.05	0.40	2.58
Yarraman QMMO 12261	1	3 1/2	0.46	1.05	0.44	0.04	0.30	0.14	109	39.45	0.43	2.44
Little Yabba Ck QMMQ 13365	1	3 5/8	0.55	1.25	0.44	0.02	0.34	0.06	134	40.74	0.52	2.40
Kenilworth QMMO 8360	3	3 1/8+ (3 1/8–3 1/4)	0.41±0.012 (0.40–0.43)	0.89±0.033 (0.82–0.92)	0.46±0.032 (0.42–0.52)	0.04±0.091 (0.02–0.05)	0.28±0.012 (0.26–0.30)	0.13±0.035 (0.07–0.12)	73.0±3.21 (68–79)	31.36±1.651 (28.09–33.37)	0.35±0.013 (0.34–0.38)	2.53±0.183 (2.16–2.71)
Mt Mee QMMO 12173	1	3 1/2+	0.47	1.09	0.43	0.03	0.30	0.10	93	32.42	0.42	2.60
Natural Bridge OMMO 10453	1	3 1/8	0.48	1.07	0.45	0.02	0.31	0.07	77	27.35	0.37	2.89
Rathdowney OMMO 10868	3	3 1/4+ (3 1/8–3 3/8+)	0.47±0.015 (0.44–0.49)	1.03±0.012 (1.01–1.05)	0.46±0.013 (0.43–0.47)	0.28±0.033 (0.21–0.31)	0.31±0.003 (0.30–0.31)	0.09±0.010 (0.07–0.10)	96.3±2.85 (93–109)	35.53±0.697 (34.68–36.91)	0.38±0.015 (0.35–0.40)	2.72±0.110 (2.59–2.94)

c. 15 km from Rathdowney on Boonah-Rathdowney Rd, SEQ, rocky outcrop, vine thicket (28°11'S, 152°46'E) (8, QMMO10868, AMC128445, Mar 1981, AM/QM-ABRS); Binna Burra, Lamington N.P., SEQ (28°12'S, 153°11'E) NVF/Palms (1, QM-MO10444, 18 Mar 1981, AM/QM-ABRS); Koreelah Ck., Beaury S.F., c. 15 km W of Urbenville, NSW (28°21'S, 152°20'E) 530 m, litter (2, AMC152151, 18 May 1976, P.H. Colman, I. Loch); c. 3 km from junction with Lever's Plateau Rd, Tartar's Creek, SEQ (28°28'S, 152°08'E), roadside gully (1, QMMO-11148, 17 Mar 1981, AM/QM-ABRS).

DIAGNOSIS

Shell minute, diameter 0.82–1.29 mm (mean 1.19 mm) with 3 1/8 to 3 3/4 (mean 3 1/2-) loosely coiled whorls, last whorl descending in front. Early spire and apex (Fig. 93c) barely elevated, SP/BWW ratio 0.06–0.22 (mean 0.11), height of shell 0.39–0.64 mm (mean 0.49). H/D ratio 0.35–0.55 (mean 0.44). Protoconch of 1 3/8 to 1 5/8 whorls, mean diameter 693.9 µm at 1 1/2 whorls. Apical sculpture (Fig. 93e,f) of widely spaced, slightly sinuous radial ribs and even finer, irregular spiral riblets. Postnuclear sculpture of crowded, protractively sinuated radial ribs, 67–134 (mean 96.70) ribs on the body whorl. Ribs/mm 24.25–40.74 (mean 31.75). Microsculpture (Fig. 93e,f) of fine radial riblets, whose apices are crenulate, 4–10 between each pair of major ribs. Umbilicus (Fig. 93b) saucer-shaped, diameter 0.34–0.57 mm (mean 0.44 mm). D/U ratio 2.16–3.31 (mean 2.41). Whorls rounded above and below the periphery. Aperture ovately lunate. Lip simple. Parietal callus developed. Colour light straw-yellow to white. Based on 28 measured adults.

No soft parts available for dissection.

RANGE AND HABITAT

In eastern Australia from just north of Rockhampton, south to near the Queensland/New South Wales border. In the northern part of its range i.e. between Biggenden and Olsen's Caves, the species lives in dry subtropical microphyll vine forest. In the south i.e. between Gympie and Natural Bridge National Park, *D. aperta* inhabits warmer moist notophyll vine forests. *D. aperta* lives among the dirt particles below the leaf litter.

REMARKS

The decision to consider all the above specimens as *D. aperta* is made reservedly. There are conchological differences between the northern and southern populations which indicate two species. However, without soft parts, recognition of two species is a tenuous proposition (Solem, 1983). *D. aperta* is probably a complex of species which represent localised experiments in miniaturisation.

Cralopa Iredale, 1941

Cralopa Iredale, 1941a, p. 267; Kershaw, 1956b, p.8; Burch, 1976, p. 132.

TYPE SPECIES

Helix stroudensis Cox 1864 ;by original designation.

PREVIOUS STUDIES

Iredale (1941a) introduced *Cralopa* for *Helix stroudensis* Cox, 1864 which has a small shell with weakly elevated spire, closed umbilicus, and numerous curved, bold radial ribs. '*Cralopa*' *intensa* Iredale, 1941 was added on the basis of small size and crowded radial postnuclear sculpture. Two new species are added here and '*C*.' *intensa* is removed to *Sinployea* Solem, 1983.

DIAGNOSIS

Shell small, diameter 1.66–3.83 mm, with 3 3/4 to 4 1/2 tightly, to loosely coiled whorls, the last descending slowly. Early spire and apex slightly elevated. Apical sculpture of prominent to bold, weakly curved radial ribs and low, narrow spiral cords. Adult sculpture of few (*carlessi*) to many (*stroudensis*), widely spaced (*carlessi*), to crowded (*kaputarensis*), bold, strongly protractively sinuated radial ribs. Microsculpture of fine radial riblets and crowded, narrow spiral cords, continuous on the major ribs. Umbilicus closed or only narrowly open. Sutures deeply impressed. Whorls round to slightly shouldered above the periphery and rounded below. Aperture roundly lunate. Lip sinuous, strongly retracted at the sutural margin to form an apertural sinus. Columella reflected over the umbilicus.

Foot short, bluntly rounded posteriorly, colour white, ommatophores white. Mantle collar with an orange glandular section extending onto the pallial roof. Kidney weakly bilobed, with pericardial lobe longer. Ureter sigmurethrous, complete, with primary arm reflexed near origin. Terminal male genitalia with a relatively expanded vas deferens, very large cylindrical penis, and weakly differentiated epiphallus. In-

TABLE 19 - RANGE OF VARIATION IN *CRALOPA* AND *ELSOTHERA* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Cralopa stroudensis	10	4 + (3 7/8–4 1/4+)	1.71 (1.45–2.22)	2.89 (2.26–3.83)	0.60 (0.52–0.67)	0.18 (0.13–0.26)	0.99 (0.77–1.19)	0.19 (0.14–0.25)	91.4 (69–109)	10.09 (7.84–13.57)	0.36 (0.29–0.43)	8.15 (7.86–8.52)
Cralopa kaputarensis	2	4 + (4 +–4 1/8+)	0.90	1.71 (1.66–1.75)	0.53 (0.52–0.54)	0.09 (0.08–0.10)	0.54 (0.53–0.55)	0.17 (0.15–0.19)	74.5 (69–80)	13.94 (12.57–15.30)		
Cralopa carlessi	22	4 1/8- (3 3/4–4 1/2)	1.84 (1.58–2.17)	3.30 (2.98–3.79)	0.56 (0.48–0.61)	0.32 (0.21–0.64)	0.97 (0.77–1.15)	0.33 (0.21–0.65)	59.1 (43–82)	5.77 (4.17–7.95)	0.56 (0.41–0.74)	5.98 (4.78–7.56)
Elsothera sericatula	8	4 1/2- (4 1/4–4 5/8+)	2.54 (2.22–2.98)	4.70 (3.96–5.58)	0.54 (0.49–0.59)	0.22 (0.13–0.43)	1.63 (1.45–1.79)	0.13 (0.09–0.25)	162 (115–190)	11.26 (9.87–13.02)	---	---
Elsothera nautiloidea	11	4 3/8+ (4 1/4–4 3/4+)	2.41 (2.17–2.81)	4.43 (4.05–5.24)	0.54 (0.50–0.57)	0.14 (0.04–0.17)	1.60 (1.45–1.83)	0.09 (0.02–0.12)	151.9 (129–190)	10.94 (10.02–11.53)	0.47 (0.41–0.62)	9.29 (7.88–10.78)
Elsothera genithecata	4	4 1/4 (4–4 5/8+)	2.94 (2.77–3.36)	5.67 (4.37–6.64)	0.53 (0.47–0.63)		1.79 (1.09–2.27)	---	132 (111–153)	7.24 (5.83–8.64)	-	

ternally, penis with apical epiphallic pore and two large, spongy longitudinal pilasters. Penial retractor muscle inserted on penis (*stroudensis*, *carlessi*), or epiphallus near penis (*kaputarensis*). Vagina relatively short. Radula with tricuspid central and lateral teeth; central tooth reduced, about 1/2 size of the laterals, cusps lanceolate, mesocone long; lateral teeth with large lanceolate mesocone.

Distribution and Ecology

The east-west distribution of *Cralopa* contrasts with the more common north-south pattern shown by other genera reviewed in this study.

Although the extensive rainforest distribution of *C. stroudensis* appears to contrast with the 'cornered' distributions of *C. kaputarensis* and *C. carlessi*, closer analysis reveals that *C. stroudensis* is also an environmentally isolated species in cool subtropical notophyll vine forests of the Great Dividing Range.

Patterns of Variation

Conchological variation is conservative and probably reflects relatively recent fragmentation of populations. It involves changes in size, spire protrusion, whorl count, rib spacing and rib number. *C. kaputarensis*, the smallest member of the genus, is a scaled down version of *C. stroudensis* with less protruded spire (SP/BWW ratios = 0.54 and 0.99 respectively) and more crowded ribs on the body whorl. *C. carlessi* is larger with greater whorl count and more elevated spire. *C. stroudensis* has the greatest number of ribs but *C. kaputarensis* has most ribs/mm. *C. carlessi* has the widest spaced ribs.

An interesting aspect of the *Cralopa* shell is the development of an apertural sinus. This is more commonly seen in New Zealand Charopidae.

Comparisons

Cralopa is most similar to *Elsothera* having shells with very similar sculpture, barely open to closed umbilicus, and relatively depressed spire. However, *Elsothera* is much larger with greater mean whorl count and higher rib count (Table 19). Furthermore *Elsothera* has an almost unilobed kidney, tapered at the apex and the primary ureter as a straight tube (Figs 109f, 105e). In contrast the kidney of *Cralopa* is weakly bilobed with the apex of the pericardial lobe and initial part of the primary ureter weakly reflexed (Figs 96e, 99e, 102). *Cralopa* has a large, cylindrical penis with two large

TABLE 20 - LOCAL VARIATION IN *CRALOPA STROUDENSIS* (COX, 1864), *CRALOPA KAPUTARENSIS* SP. NOV. AND *CRALOPA CARLESSI* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Cralopa stroudensis												
Stroud AMC 63500 (Holotype)	1	4	1.62	2.56	0.63	0.21	0.94	0.23	109	13.57	0.31	8.30
Yessabah Caves AMC 121680	2	4+ (3 7/8–4 1/8+)	2.05±0.175 (1.87–2.22)	3.62±0.210 (3.41–3.83)	0.57±0.015 (0.55–0.58)	0.26	1.11±0.085 (1.02–1.19)	0.23±0.014 (0.21–0.25)	95.0±11.00 (84–106)	8.32±0.475 (7.84–8.79)	0.43	7.90
Goomburra S.F. QMMO 12695	1	3 7/8	1.45	2.26	0.64	0.17	0.77	0.22	69	9.72	0.29	7.86
Koreelah S.F. QMMO 10954	2	(4 1/8–4 1/4+)	1.64–0.020 (1.62–1.66)	2.49±0.060 (2.43–2.56)	0.66±0.010 (0.65–0.67)	0.15±0.020 (0.13–0.17)	0.94	0.16±0.020 (0.14–0.18)	70	9.17	---	---
Bunya Mts QMMO 16851	4	4–4 1/4-	1.67±0.055 (1.58–1.83)	2.96±0.122 (2.73–3.19)	0.57±0.015 (0.52–0.58)	0.16±0.010 (0.13–0.17)	1.03±0.052 (0.94–1.15)	0.16±0.009 (0.14–0.18)	96.3 (90–106)	10.42±0.704 (9.06–12.37)	0.38±0.010 (0.37–0.39)	8.36±0.165 (8.19–8.52)
Cralopa kaputarensis												
Mt Kaputar OMMO 16753 (Holotype)	1	4+	0.90	1.66	0.54	0.08	0.53	0.15	80	15.30	---	---
OMMO 16750	1	4 1/8+	0.90	1.75	0.52	0.10	0.55	0.19	69	12.57	---	---
Cralopa carlessi												
Inverell AMC 123538 (Holotype)	1	4 1/2	2.04	3.62	0.56	0.43	1.07	0.40	70	6.15	---	---
AMC 123610	3	4+ (3 7/8–4 1/8)	1.80±0.027 (1.75–1.83)	3.32±0.026 (3.28–3.37)	0.54±0.006 (0.53–0.55)	0.27±0.038 (0.21–0.34)	0.98±0.023 (0.94–1.02)	0.28±0.054 (0.21–0.36)	72.3±4.73 (67–82)	6.93±0.510 (6.41–7.95)	---	---
AMC 3640	9	4+ (3 7/8–4 1/4-)	1.81±0.059 (1.62–2.17)	3.21±0.064 (2.98–3.54)	0.56±0.014 (0.49–0.61)	0.27±0.018 (0.21–0.34)	0.98±0.029 (0.89–1.15)	0.28±0.016 (0.21–0.36)	60.1±2.92 (48–75)	6.03±0.241 (5.14–6.91)	0.44±0.013 (0.41–0.45)	7.26±0.170 (6.97–7.56)
Attunga AMC 28496	2	4 1/2	2.07–0.025 (2.04–2.09)	3.67±0.125 (3.54–3.79)	0.57±0.025 (0.54–0.57)	0.39±0.045 (0.34–0.43)	1.00±0.020 (0.98–1.02)	0.38±0.049 (0.33–0.43)	57.5±1.50 (56–59)	5.01±0.305 (4.70–5.31)	0.67±0.010 (0.66–0.68)	5.49±0.028 (5.21–5.77)
Wee Jasper AMC 142961	1	3 7/8	1.58	2.98	0.48	0.38	0.85	0.51	45	4.80	0.51	5.81
Tuglow Caves AMC 124279	4	4 1/8- (3 3/4–4 1/2-)	1.84±0.122 (1.58–2.17)	3.20±0.194 (2.64–3.54)	0.58±0.016 (0.55–0.61)	0.43±0.074 (0.30–0.64)	0.89±0.047 (0.77–0.98)	0.48±0.060 (0.39–0.65)	46.3±3.33 (43–53)	4.81±0.320 (4.17–5.18)	0.61±0.048 (0.51–0.74)	5.30±0.210 (4.78–5.70)
Wumbeyan Caves AMC 142967	2	4- (3 3/4–4 1/8)	1.83±0.130 (1.70–1.96)	3.56±0.235 (3.32–3.79)	0.52±0.005 (0.51–0.52)	0.26±0.045 (0.21–0.30)	1.01±0.065 (0.94–1.07)	0.26±0.025 (0.23–0.28)	55	5.26		--

longtitudinal pilasters (Figs 96b, 99b, 102b) in contrast to *Elsothera* which has a pear-shaped penis internally divided by an apical collar (Figs 105e, 109b). The epiphallus - vas deferens junction of *Elsothera* is highly modified (Figs 105b, 109a) while that of *Cralopa* is scarcely differentiated (Figs 96a, 99a, 102e). *Egilomen globosa* also has prominent radial ribs and a closed umbilicus but differs in having beaded microsculpture (Figs 128g, 131f).

Cralopa stroudensis (Cox, 1864)
(Figs 95–97; Tables 19, 20)

Helix stroudensis Cox, 1864, p. 20; Tryon, 1887, p. 25, pl. 4, figs. 28, 29.

Gyrocochlea stroudensis (Cox); Hedley, 1924, p. 217, pl. 31, figs 25–27; Iredale, 1937a, p. 323.

Cralopa stroudensis (Cox); Iredale, 1941a, p. 269.

COMPARISONS

C. stroudensis can be distinguished from its congeners by high rib count, relatively large size and moderate spire elevation. *C. kaputarensis* is smaller, has a lower rib count and almost flat spire (Fig. 98c). *C. carlessi* is larger with reduced rib count and strongly elevated spire (Fig. 101c). Anatomically the differences are subtle. *C. stroudensis* (Fig. 96b) has a large cylindrical penis with two unequal, longitudinal pilasters, and a penial retractor muscle inserted on the penis apex; *C. kaputarensis* (Fig. 99b) has a large penis with two large longitudinal pilasters which anastomose and divide into smaller pilasters basally, and a penial retractor muscle which is inserted on the epiphallus; *C. carlessi* (Fig. 102b) has the penial retractor muscle inserted on the penis which has two slender equal pilasters and a low central pustular swelling internally.

TYPE MATERIAL

HOLOTYPE: AMC63500, Stroud, NSW. Coll. Rev. R.L. King. Height 1.62 mm, diameter 2.56 mm, H/D ratio 0.63, D/U ratio 8.30, whorls 4.

PARATYPES: AMC225, 4 specimens, same data as holotype.

OTHER MATERIAL

Sherrard Falls, Dorrigo, NSW, 600 m, warm temperate rainforest, in litter (1, QMMO16778, 13 Nov 1983, AM/QM - ABRS); c. 28.5 km from Goomburra, on Goomburra S.F. road, SEQ (27°59'S, 152°21'E) 600 m CNVF/Palms (8, QMMO12695, QMMO11128, AMC136816, 7 Dec 1981, AM/QM - ABRS); Yessabah Limestone Cave, Sherwood Quarry, W of Kempsey NSW (31°06'S, 152°42'E) ground litter, in and out of cave (2, AMC121680, 9 Oct. 1979, P.H. Colman, J. Stanisic); Lower Ballanjui Falls Circuit, Binna Burra, Lamington N.P., SEQ, NVF, litter (1, QMMO16893, J. Stanisic, D. Potter, J. Chaseling); Bunya Nts N.P. (27°53'S, 151°33'E) NVF (1, QMMO6072, QMMO6278, 5 Mar 1976, M.J. Bishop); initial part of Kweebani Caves walk, Binna Burra, Lamington N.P., SEQ NVF, under log (1, QMMO16888, 9 Mar 1984 J. Stanisic); top of Condamine River Valley, SEQ (28°15'S, 152°29'E) (2, QMMO10410, AMC128902, Mar 1981, AM/QM - ABRS); Cherry Plain - Westcott Plain Circuit, Bunya Mts N.P., SEQ, NVF/MVF, under logs (43, QMMO16857, 6 Nov 1985, J. Stanisic, D. Potter); Dandabah, Bunya Mts N.P., SEQ, NVF/under logs (13, QMMO16846, 12 May 1984, J. Stanisic, D. Potter); Big Falls Circuit Bunya Mts N.P., SEQ, SNVF, under logs (27, QMMO16851, 5 Nov 1985, J. Stanisic, D. Potter); Halls Plain, E of Emu Vale, SEQ, CNVF, under log (1, QMMO16891, 4 May 1986, J. Stanisic, J. Chaseling); Cunningham's Gap N.P., SEQ, near monument, 755 m, (28°04'S, 152°24'E) SNVF/Ferns (1, QMMO12685, 7 Dec 1981, AM/QM - ABRS); c. 18 km from Legume, on Acacia Plateau Rd, Koreelah S.F., SEQ., SEVT, NVF, MVF (1, QMMO12718, 8 Dec 1981, AM/QM - ABRS); Bellengen River S.F., NSW (30°25'S, 152°44'E) dense rainforest (1, QMMO10814, AMC128389, 12 Mar, 1981, AM/QM - ABRS); Bunya Mts N.P., SEQ (13, AMC63869, 8 Feb 1961, D.F. McMichael); Rocky Ck, Red Scrub Flora Reserve, NSW (28°38'S, 153°20'E) (1, AMC128867, 20 Mar 1981, AM/QM - ABRS); Port Macquarie (1, AMC36564, ex Hedley); Dandabah, Bunya Mts, SEQ (26°53'S, 151°36'E) (158, QMMO12281, AMC136605, 31 Sept 1982, AM/QM - ABRS); Port Macquarie (1, AMC63855, ex Cox); Koreelah S.F., NSW, SEVT/MVF (28°21'S, 152°24'E) (11, AMC128557, QMMO10954 15 Mar 1981, AM/QM - ABRS); Natural Arch, Carrai Caves, near Kempsey, NSW, litter (1, AMC152198, 22 Feb 1980, P.H. Colman).

DIAGNOSIS

Shell diameter 2.26–3.83 mm (mean 2.89 mm) with 3 7/8 to 4 1/4+ (mean 4+) loosely coiled whorls. Apex and early spire (Fig. 95a) slightly elevated. SP/BWW ratio 0.14–0.25 (mean 0.19), height 1.45–2.22 mm (mean 1.71 mm). H/D ratio 0.52–0.67 (mean 0.60). Last whorl descending much more rapidly. Protoconch of 1 1/2 to 1 5/8 whorls, mean diameter 593.3 μm at 1 1/2 whorls. Apical sculpture (Fig. 95d) of numerous, high, curved radial ribs, becoming slightly more crowded toward the nuclear-post

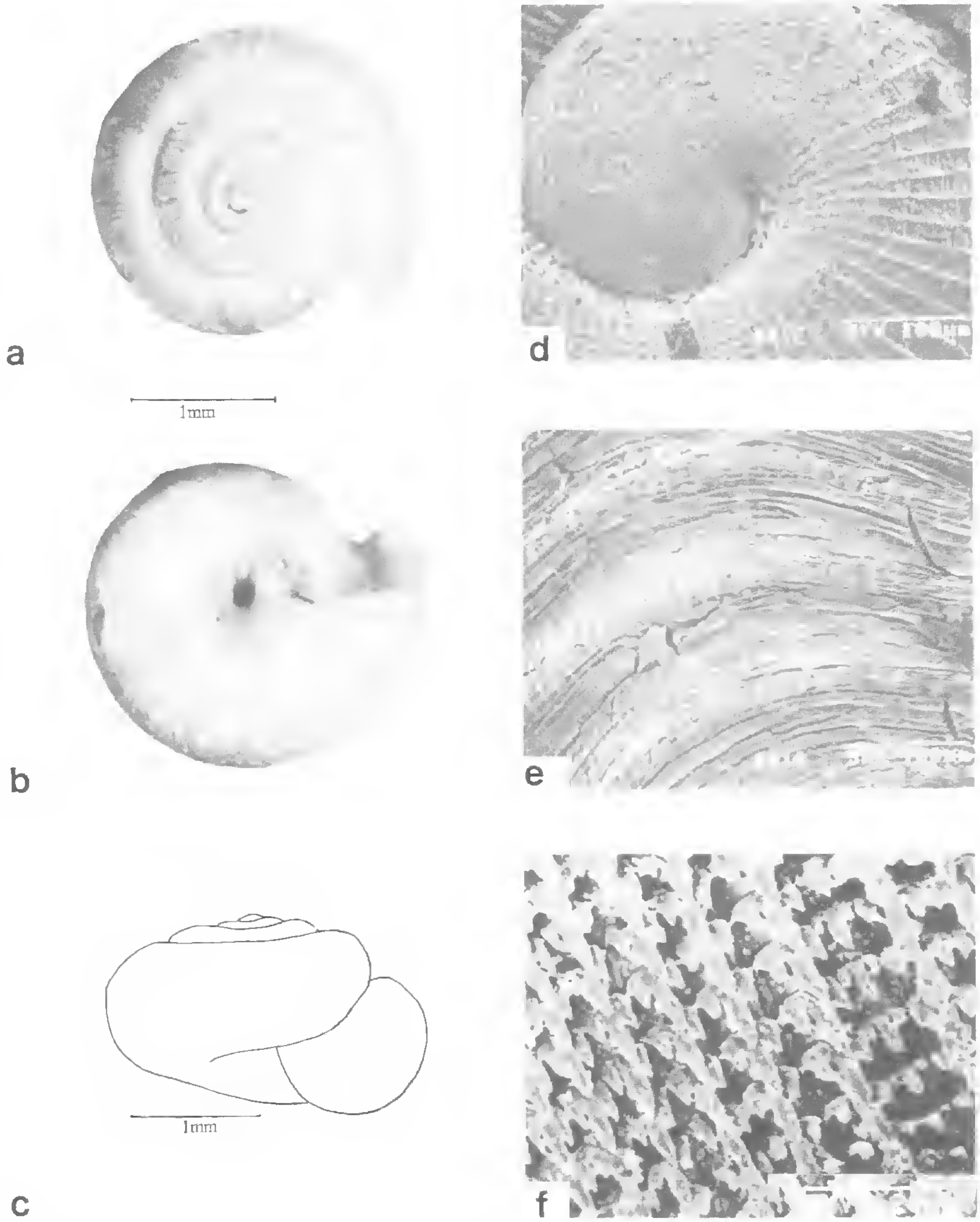


FIG. 95. *Cralopa stroudensis* (Cox, 1864). a–c, Stroud, NSW. AMC63500, holotype; d–f, Dandabah, Bunya Mts, SEQ. QMMO12281. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, central and lateral teeth. Scale lines as marked.

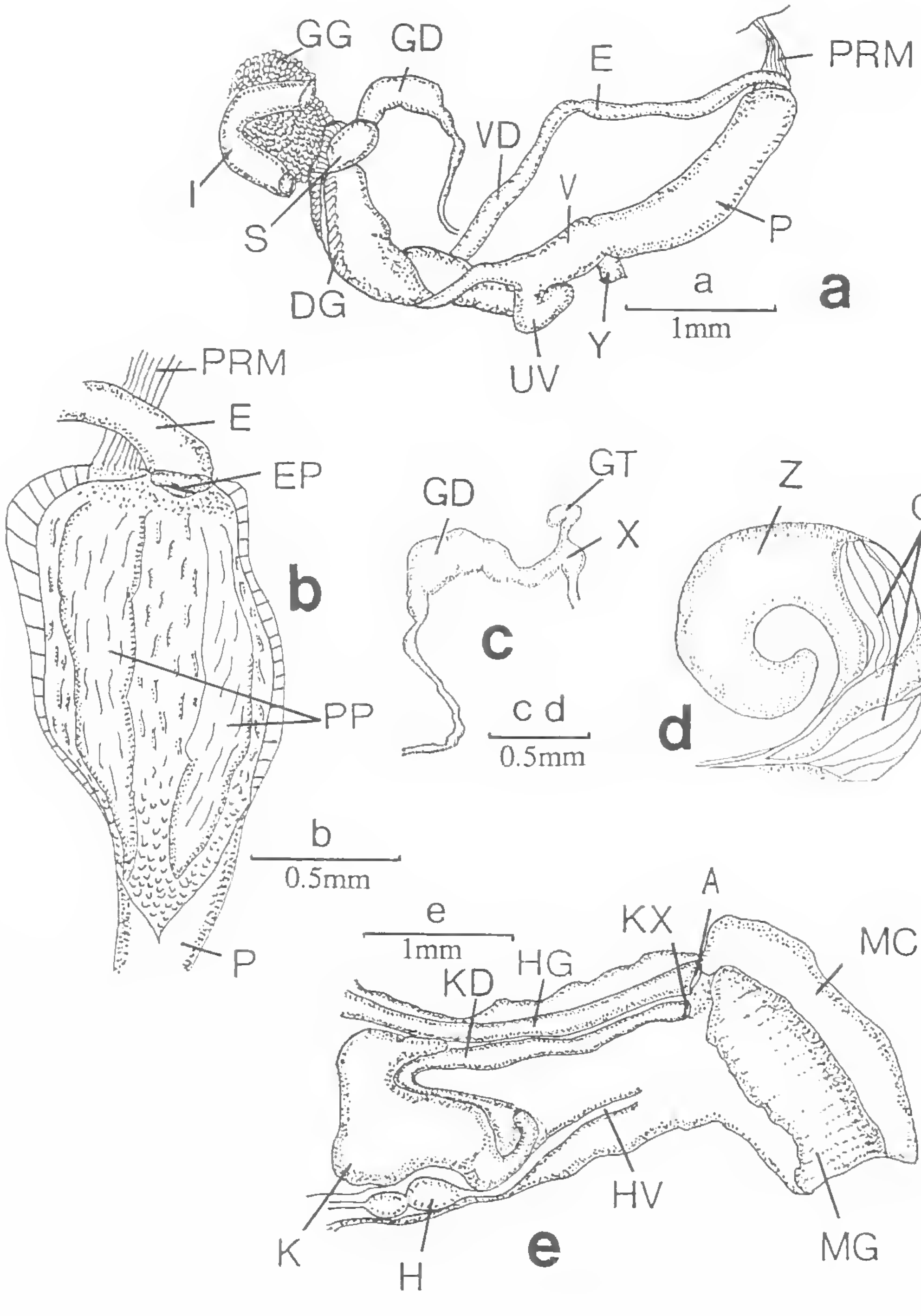


FIG. 96. *Cralopa stroudensis* (Cox, 1864). Dandabah, Bunya Mts N.P., SEQ. QMMO12281. a, genitalia; b, penis interior; c, hermaphroditic duct, carrefour and talon; d, ovotestis; e, pallial cavity. Scale lines as marked.

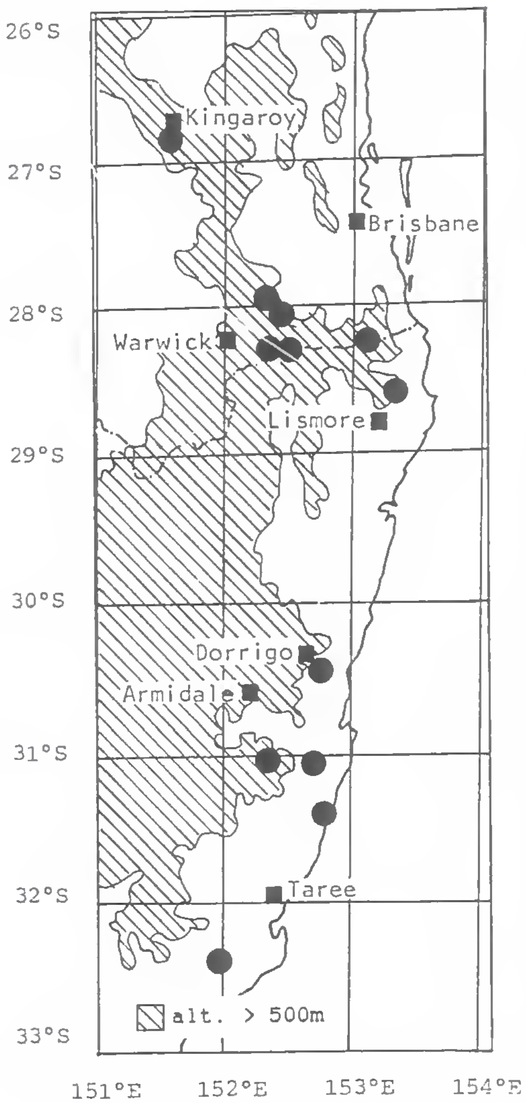


FIG. 97. Distribution of *Cralopa stroudensis* (Cox, 1864).

nuclear junction, crossed by fine spiral cords. Post nuclear sculpture (Fig. 95e) of numerous, large, strongly protractively sinuated radial ribs 69–109 (mean 91.4) ribs on the body whorl. Ribs/mm 7.84–13.57 (mean 10.08). Microsculpture (Fig. 95e) of fine radial riblets, 3–10 between each pair of major ribs, crossed by numerous, regularly spaced spiral cords. Umbilicus (Fig. 95b) very small to closed, diameter 0.29–0.43 mm (mean 0.36 mm), D/U ratio 7.86–8.52 (mean 8.15). Sutures deep; whorls slightly shouldered above and rounded below the periphery (Fig. 95c). Aperture roundly lunate. Lip sinuous, strongly retracted at the sutural margin and forming an apertural sinus. Columella expanded and slightly channelled in older specimens, weakly reflected over the umbilicus. Parietal callus developed. Colour variable, white through straw-yellow to light-brown. Based on 10 measured adults.

Epiphallus (Fig. 96a) not strongly differentiated from the vas deferens, entering the penis apically through a simple pore (Fig. 96b) surrounded by fleshy thickenings. Penis (Fig. 96b), internally with two large, unequal longitudinal pilasters, and a series of low, longitudinally arranged pustulations. Penial retractor muscle inserting on the penis head adjacent to the epiphallus. Free oviduct (Fig. 96a) very long, twisted and muscularised, internally with a spongy pad-like thickening. Vagina long with internal lamellar thickenings.

Radula (Fig. 95a) as for genus.

Based on two dissected specimens (QMMO-12281).

RANGE AND HABITAT

Cool subtropical notophyll vine forests of the Great Dividing Range between Barrington Tops, NSW and Bunya Mts, SEQ; the McPherson Ranges of the QLD/NSW border; and the limestone ridge which extends intermittently from Yessabah to Carrai, W of Kempsey, NSW. *C. stroudensis* lives under logs and sometimes occurs in large numbers per site.

REMARKS

There is significant conchological variation between populations. However insufficient material is available to investigate its extent. The Yessabah Cave shells (AMC121680) are noticeably larger, possibly due to the abundant supply of calcium for shell construction.

Cralopa kaputarensis sp. nov.
(Figs 98–100; Tables 19, 20)

ETYMOLOGY

For the type locality, Mt Kaputar.

COMPARISONS

Cralopa kaputarensis is separated from *C. stroudensis* in discussion of that species above. The barrel-shaped penis is a conspicuous character which identifies *C. kaputarensis*. *C. car-*

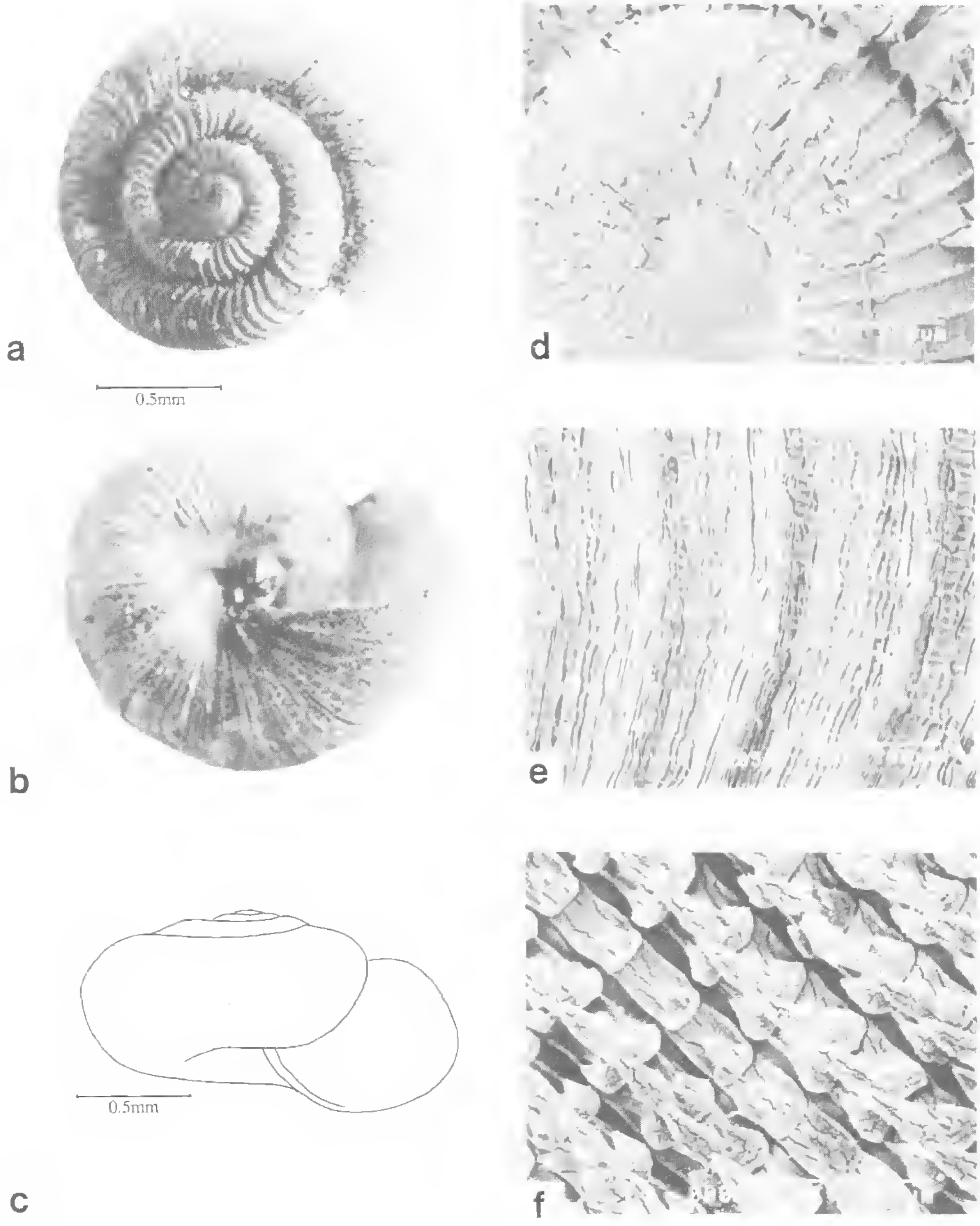


FIG. 98. *Cralopa kaputarensis* sp. nov. a–c, Summit, Mt Kaputar, NSW. QMMO16753, holotype; d–f, Dawson Springs, Mt Kaputar, NSW. QMMO16742, paratypes. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, central and lateral teeth. Scale lines as marked.

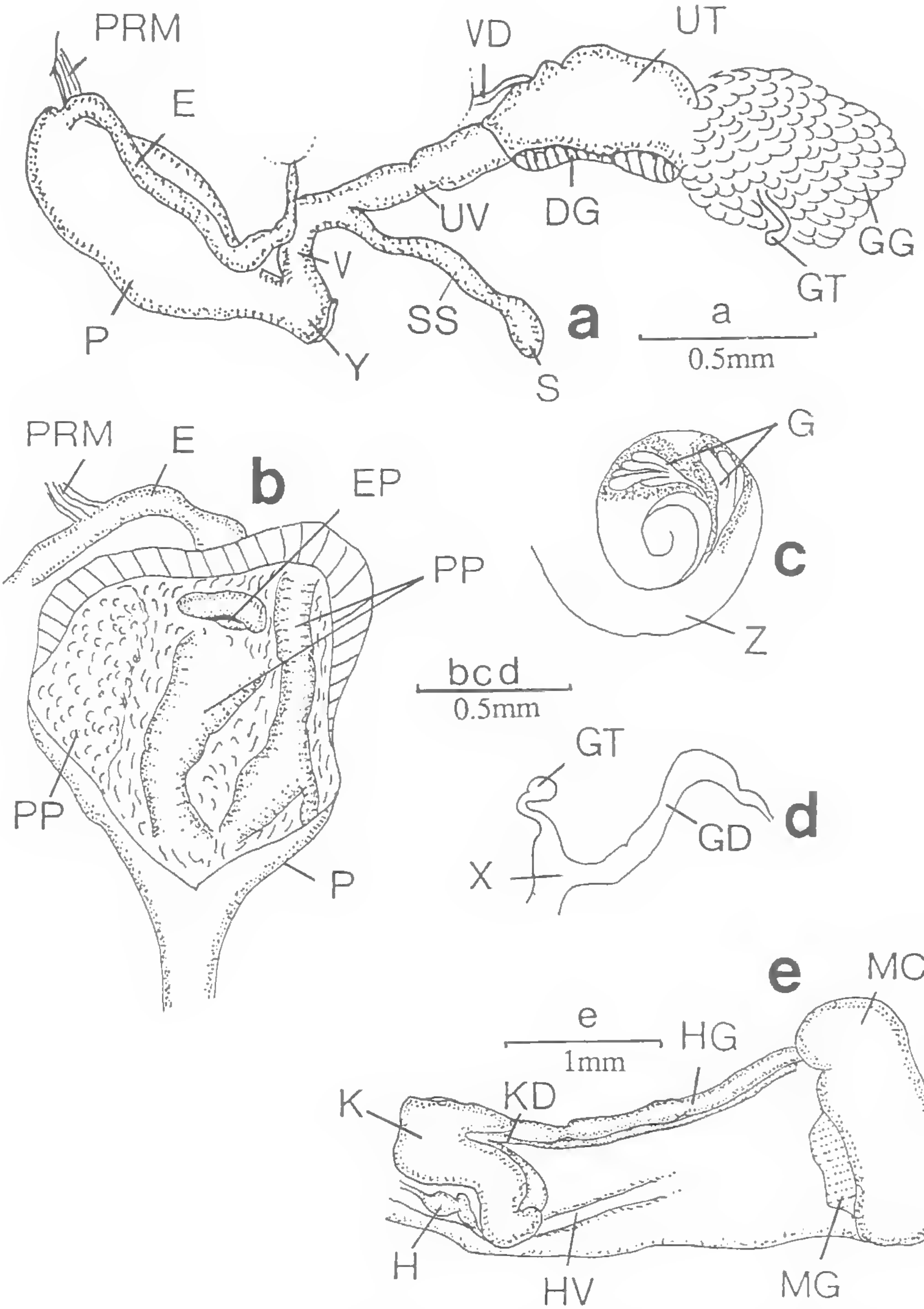


FIG. 99. *Cralopa kaputarensis* sp. nov. Dawson Springs, Mt. Kaputar, NSW. QMMO16742, paratype. a, genitalia; b, penis interior; c, ovotestis; d, talon, carrefour and hermaphroditic duct; e, pallial cavity. Scale lines as marked.

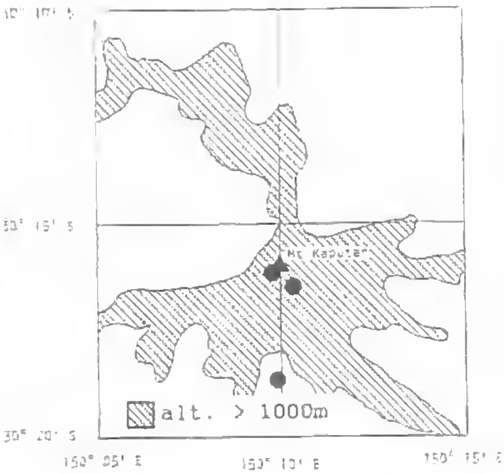


FIG. 100. Distribution of *Cralopa kaputarensis* sp. nov. on the Mt Kaputar Plateau.

lessi is much larger with more elevated spire and flatter whorls.

TYPE MATERIAL

HOLOTYPE: QMMO16753, summit, Mt Kaputar, NSW, 1500 m, among rocks, grass and litter. Collected 9 Nov 1983, AM/QM - ABRS. Height 0.90 mm, diameter 1.66 mm, H/D ratio 0.54, whorls 4+.

PARATYPES: Dawson Springs, Mt Kaputar, NSW, 1300 m, under logs, in fern gully (3, QMMO16742, 8 Nov 1983, AM/QM - ABRS); Joker's Spring, Mt. Kaputar, NSW, 1000 m, edges of rocky creek bed, among lichen (1, QMMO16750, 8 Nov 1983, AM/QM - ABRS).

DIAGNOSIS

Shell diameter 1.66–1.75 mm (mean 1.71 mm), with 4+ to 4 1/8+ (mean 4+) loosely coiled whorls, last descending slowly. Early spire and apex (Fig. 98a) very slightly elevated, SP/BWW ratio 0.15–0.19 (mean 0.17), height 0.90 mm. Protoconch of 1 1/2 whorls, mean diameter 734.0 μm at 1 1/2 whorls. Apical sculpture (Fig. 98d) of slightly curved, radial ribs and fine low spiral cords, more noticeable toward the sutures. Postnuclear sculpture (Fig. 98c) of large, crowded, strongly protractively sinuated radial ribs, 69–80 (mean 74.5) ribs on the body whorl. Ribs/mm 12.57–15.30 (mean 13.94). Microsculpture (Fig. 98e) of fine radial riblets, 6–10 between each pair of major ribs, crossed by crowded, regularly spaced, low spiral cords. Umbilicus (Fig. 98b) reduced to a slender crack, more open in sub-adult specimens. Sutures impressed. Whorls rounded above and below the periphery (Fig. 98c). Aperture roundly lunate. Lip sinuate, retracted at the sutural margin to form an apertural sinus. Columella dilated and reflected over the umbilicus. Parietal callus well developed. Colour dark brown. Based on 2 measured adults.

Vas deferens a thin tube, giving rise to a weakly differentiated epiphallus. Epiphallus entering penis apically through a simple pore. Penis broadly tubular, internally with two large longitudinal pilasters which anastomose, and divide into numerous smaller pilasters basally. Penial retractor muscle (Fig. 99b) inserted on the epiphallus. Female reproductive system small compared with the penis.

Radula (Fig. 98f) with central tooth much smaller than laterals. Based on one dissected specimen (QMMO16742).

RANGE AND HABITAT

Only on the Mt Kaputar Plateau, near Narrabri, NSW. Under logs, rocks, and among lichen on the edges of springs.

REMARKS

C. kaputarensis is closely related to *C. stroudensis* and is probably a recent derivative.

Cralopa carlessi sp. nov.
(Figs 101–103: Tables 19,20)

ETYMOLOGY

For Terry Carless who collected specimens for this study.

COMPARISONS

The flatter more loosely coiled whorls, elevated spire and reduced number of radial ribs on the body whorl characterise *C. carlessi*. *C. kaputarensis* has an almost flat spire (Fig. 98c) and is much smaller (Table 19).

TYPE MATERIAL

HOLOTYPE: AMC123538, Inverell, NSW. Collected by C.T. Musson, 1889. Height of shell 2.04 mm, diameter 3.62 mm, H/D ratio 0.56, whorls 4 1/2.

PARATYPES: AMC153716, 2 specimens, same collection data as holotype: Hills of Glenrock Stn, NSW (31°41'S, 151°24'10"E) alt. c. 600 m, under logs and limestone slabs and litter, dry, semi-open scrub (2, AMC144200, 17 Jun 1984, P.H. Colman); Wombeyan Caves, W of Mittagong, NSW, steep scrub and grass covered limestone slope, in litter outside large

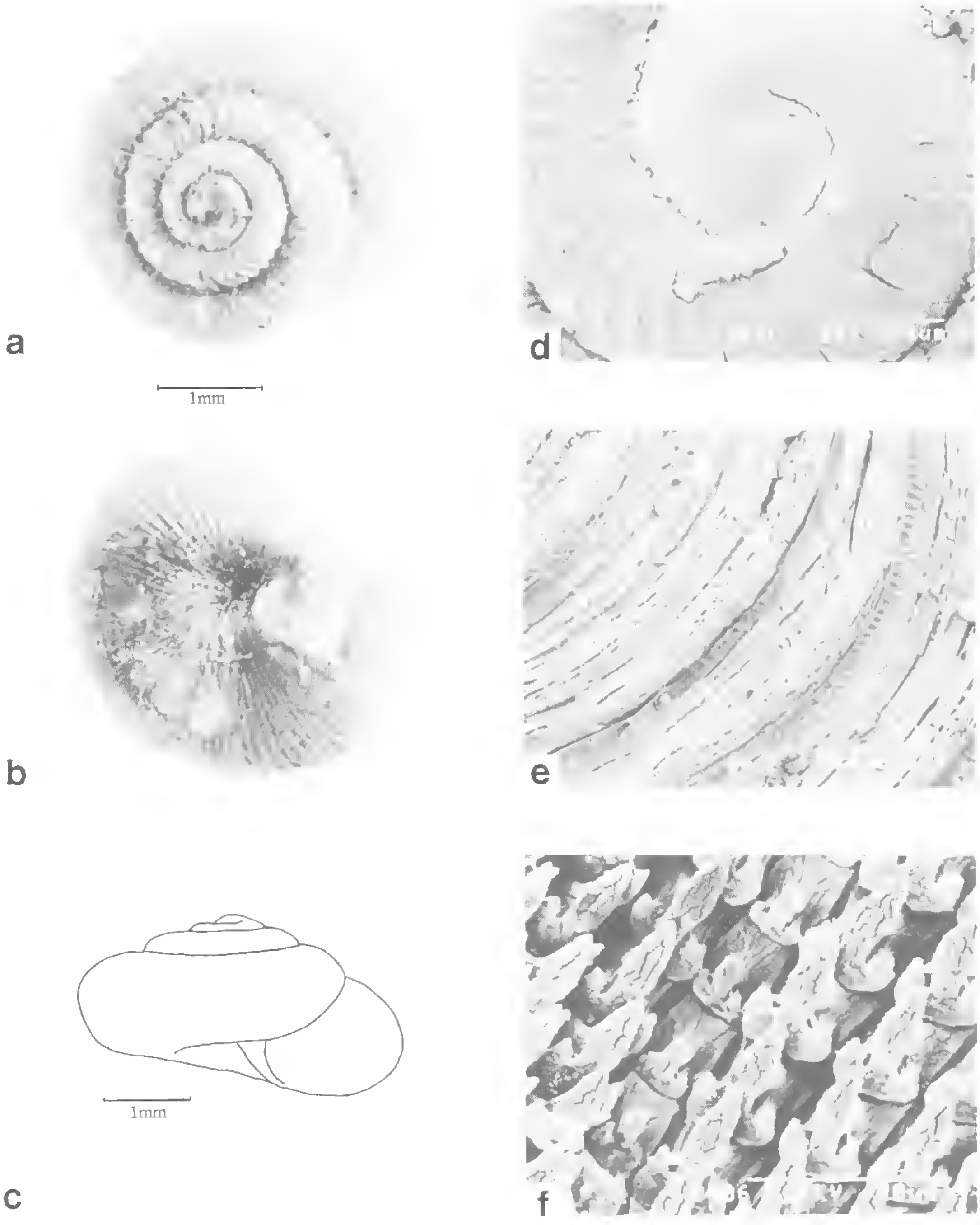


FIG. 101. *Cralopa carlessi* sp. nov. a–c, Inverell, NSW. AMC123538, holotype; d–e, Hills of Glenrock Stn, NSW. AMC144200, paratype; f, Inverell, NSW. AMC3640, paratype. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, central and lateral teeth. Scales lines as marked.

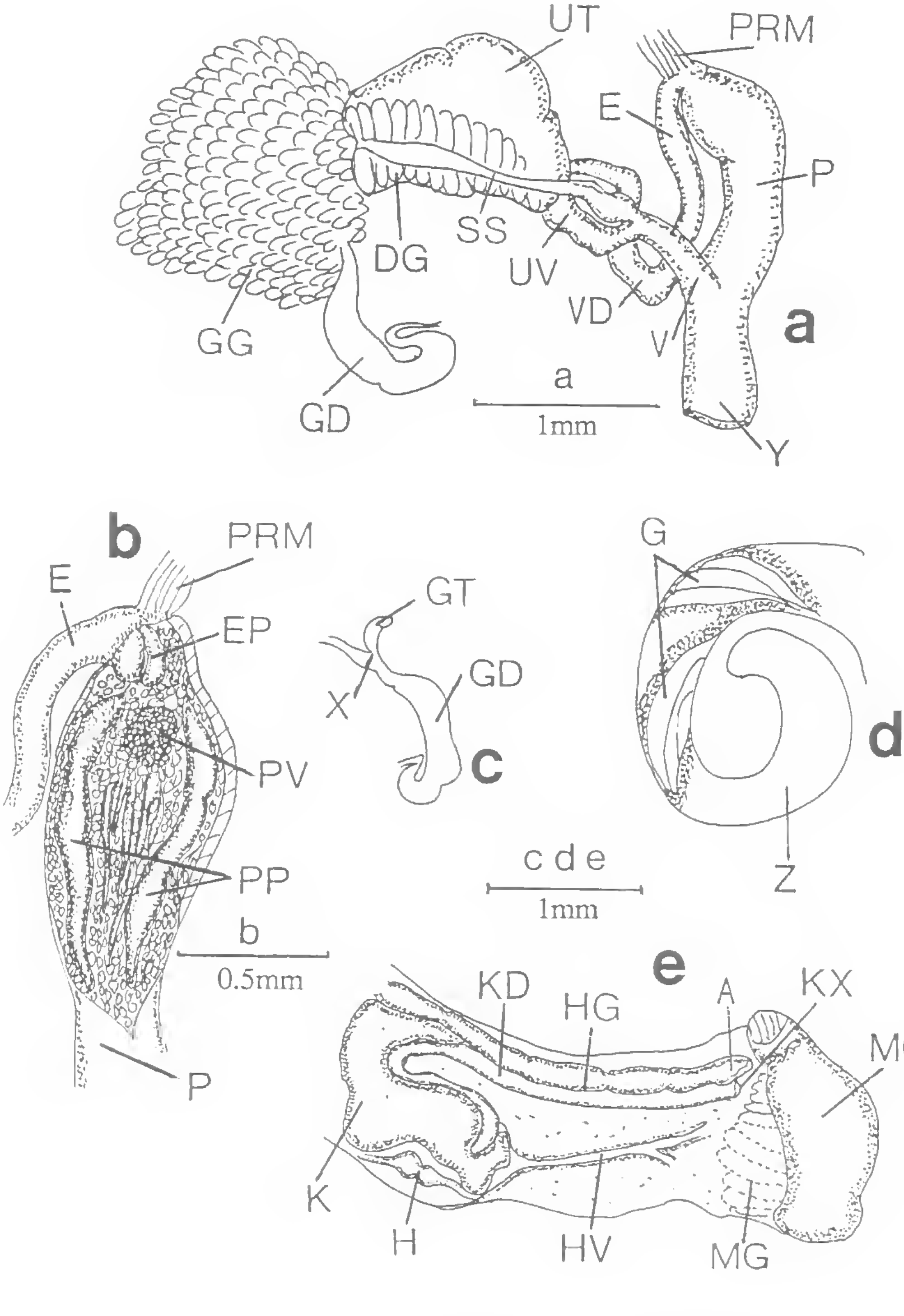


FIG. 102. *Cralopa carlessi* sp. nov. Hills of Glenrock Stn, NSW. QMMO144200, paratype. a, genitalia; b, penis interior; c, talon and hermaphroditic duct; d, ovotestis; e, pallial cavity. Scale lines as marked.

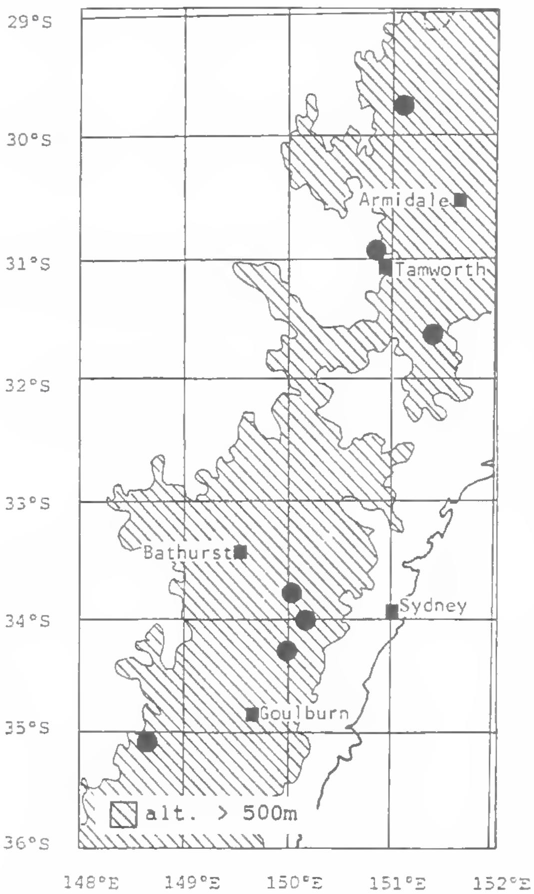


FIG. 103. Distribution of *Cralopa carlessi* sp. nov.

cave (2, AMC142967, 28 Dec 1981, M. Shea); West side Kowmung River at Gridiron Bends, near Tuglow Caves, NSW, in litter and soil on limestone bluffs (7, AMC124279, 12 Dec 1979, W.F. Ponder, P.H. Colman); Attunga, NSW (2, AMC28496, C. Laseron); Inverell, NSW (3, AMC123610, C.T. Musson); Inverell, NSW (11, AMC3640, W.S. Duncan); c. 1 km N of Wee Jasper, NSW, on Careys Caves Rd, in limestone scrub (2, AMC142961, 20 Oct 1980, P.H. Colman, J. Hall).

Other Material

Entrance to Devil's Coachhouse, Jenolan Caves, NSW, litter (2, QMMO17295, 13 Dec 1979, J. Stanisic).

Diagnosis

Shell diameter 2.98–3.79 mm (mean 3.30 mm) with 3 3/4 to 4 1/2 (mean 4 1/8) loosely coiled whorls, last descending more rapidly. Apex and early spire (Fig. 101b) very slightly to moderately elevated, SP/BWW ratio 0.21–0.64 (mean 0.33), height 1.58–2.17 mm (mean 1.84 mm), H/D ratio 0.48–0.61 (mean 0.56). Protoconch of 1 3/8 to 1 5/8 whorls, mean diameter 727.3 μm at 1 1/2 whorls. Apical sculpture (Fig. 101d) of thin, curved, regularly spaced radial ribs, crossed by low spiral cords. Postnuclear sculpture (Fig. 101e) of numerous large, strongly protractively sinuated radial ribs, 43–82 (mean 59.1) ribs on the body whorl. Ribs/mm 4.17–7.95 (mean 5.77). Microsculpture (Fig. 101e) of fine radial riblets, 6–12 between each pair of major ribs, and fine crowded spiral cords which are higher at their intersection with the radials, producing a beaded effect. Sculpture continuous on the base. Umbilicus (Fig. 101b) narrow, D/U ratio 4.78–7.56 (mean 5.98), diameter 0.41–0.74 mm (mean 0.56 mm), reduced to a lateral crack, or closed by the columellar reflection. Sutures impressed. Whorls rounded above and below the periphery (Fig. 101c). Aperture ovately lunate. Lip sinuous, thickened at the columellar edge. Columella dilated, reflected over the umbilicus, retracted at the suture to form a small sinus. Parietal callus developed. Colour yellowy-brown. Based on 22 measured adults.

Epiphallus (Fig. 102a) weakly differentiated from vas deferens, entering penis apically through a pore surrounded by fleshy thickenings. Penis (Fig. 102b) cylindrical, without a sheath, internally with two slender equal longitudinal pilasters and an apical spongy thickening which may act as a verge, otherwise pustulose. Penial retractor muscle inserting on the penis head. Vagina tubular, about as long as the free oviduct. Atrium relatively long.

Radula (Fig. 101f) as for genus.

Based on one dissected specimen (AMC144200).

Range and Habitat

Confined to a series of isolated limestone outcrops on the western edge of the Great Dividing Range, from north of Goulburn to north of Tamworth, NSW; under logs and rocks and among soil and litter.

Remarks

Various populations of *C. carlessi* show some notable variation in shell characters (Table 20). However the patterns are largely mosaic and probably reflect differences in isolated populations. In contrast, specimens from the Tuglow Caves (AMC124279) have a more elevated spire and more open umbilicus which are uncorrelated changes that may indicate speciation trends in distant populations.

Elsothera Iredale, 1933

Elsothera Iredale, 1933, p. 53; Iredale, 1937a, p. 324; Iredale, 1941a, p. 267; Kershaw, 1956a, p.140; Burch, 1976, p. 132.

TYPE SPECIES

Helix sericatula Pfeiffer, 1850, by original designation.

PREVIOUS STUDIES

Elsothera was introduced for *Helix sericatula* Pfeiffer, 1850 from the Sydney region, NSW. Iredale (1937a, 1939) added 9 species from southern Australia, and Kershaw (1956a) another 3 from Victoria based on shell features. A number of generic groups may be represented in *Elsothera* but this matter is beyond the scope of the present study. *Elsothera* is redefined to include *H. sericatula* and two species from northeast NSW and SEQ.

DIAGNOSIS

Diameter 3.96–6.64 mm, with an average of 4 1/4 to 4 3/4+ normal to loosely (*genithecata*) coiled whorls. Apex and early spire flat (*genithecata*) to slightly elevated. Apical sculpture of crowded, weakly curved, high radial ribs and finer, more crowded, low spiral cords which continue unto the radial ribs. Radials vague to absent on initial part of protoconch. Adult sculpture of numerous, very crowded, high, protractively sinuated radial ribs. Microsculpture of fine, high radial riblets and equally high, narrow, more widely spaced spiral cords. Umbilicus closed to barely open (*nautilodea*). Sutures impressed to distinctly channelled (*genithecata*). Whorls shouldered above and rounded below a weakly compressed periphery, last inflated and sometimes (*nautilodea*) with a weak supraperipheral sulcus. Lip simple, columellar margin reflected over the umbilicus. Colour light to dark-brown with darker radial streaks.

Terminal male genitalia with long, muscularised epiphallus, sometimes partially sheathed (*genithecata*), entering penis through a simple pore surrounded by a collar. Epiphallus-vas deferens junction swollen, complex with vas entering laterally. Penis short, tubular with apical bulb, internally with a spongy or fleshy collar constricting the entrance to the main penis chamber. Penial bulb with numerous short, transverse (*sericatula*) or longitudinal (*genithecata*) pilasters. Penis proper with short, longitudinal thickenings and pustulations (*genithecata*), or only pustulations (*sericatula*). Vagina short, or long with an apical caecum (*genithecata*). Radula with tricuspid central and lateral teeth, central smaller; laterals with very large broad lanceolate mesocone.

DISTRIBUTION AND ECOLOGY

Elsothera has a wide distribution from just north of the NSW/QLD border to south of Sydney, NSW. It is one of the few groups of east-coast charopids which inhabits drier, open forest. *E. sericatula* inhabits wet and dry sclerophyll forest and *E. genithecata*, has been found in 'open eucalypt forest' in the Upper Richmond Range, NSW. Ability to adapt to drier environments gives *Elsothera* the opportunity to exploit a vast amount of relatively snail depauperate habitat. The genus is quite probably more widespread than is indicated by the coverage presented here and detailed statements about distribution are inappropriate at this time. Life-styles of the three species reviewed are diverse, probably reflecting the overall adaptability of the genus.

COMPARISONS

Elsothera has a shell with average number of whorls and numerous, weakly, protractively sinuated radial ribs. In contrast the conchologically similar *Cralopa* has fewer whorls and fewer, bolder radial ribs which are strongly protractively sinuated. Radular characteristics of the two genera are similar. The constricting penial collar, vague penial pilasters, complex vas deferens-epiphallus junction, epiphallic sheath and vaginal caecum of *Elsothera* are all significant differences from the *Cralopa* pattern of simple penis with large longitudinal pilasters, barely differentiated epiphallus, and lack of additive structures.

REMARKS

Elsothera is most likely a rainforest-adapted group which has managed to colonise drier forests. The large brown radially ribbed shell and unilobed elongate kidney are characteristics of other rainforest genera such as *Gyrocochlea* and *Nautiliropa*. Large size, combined with a complete secondary ureter were probably important preadaptations which have enabled *Elsothera* to exploit drier habitats.

TABLE 21 - LOCAL VARIATION IN *ELSOTHERA SERICATULA* (PFEIFFER, 1850), *ELSOTHERA NAUTILODEA* (COX, 1866) AND *ELSOTHERA GENITHECATA* SP NOV (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Elsothera sericatula												
Australia												
BMNH 1987055 (Lectotype)	1	4 1/2	2.39	4.64	0.51	0.17	1.58	0.11	190	13.02	—	—
BMNH 1987055	3	4 1/4+ (4 1/4–4 3/8-)	2.29±0.035 (2.22–2.34)	4.00±0.026 (3.96–4.05)	0.57±0.012 (0.55–0.59)	0.18±0.027 (0.13–0.21)	1.49±0.023 (1.45–1.53)	0.12±0.017 (0.09–0.14)	144.7±5.04 (135–152)	11.49±0.330 (10.84–11.95)	—	—
Shark Island AMC 103604	5	4 1/2+ (4 1/4–4 5/8+)	2.73±0.089 (2.43–2.98)	5.13±0.117 (4.94–5.58)	0.53±0.010 (0.49–0.55)	0.25±0.047 (0.17–0.43)	1.72±0.023 (1.66–1.79)	0.15±0.027 (0.10–0.25)	168.0±6.18 (136–183)	10.65±0.345 (9.87–11.39)	—	—
Elsothera nautilodea												
Clarence River AMC 136903 (Lectotype)	1	4 3/4-	2.81	5.24	0.54	0.13	1.63	0.07	190	11.53	—	—
Harwood Island AMC 152174	10	4 3/8- (4 1/4–4 5/8-)	2.37±0.049 (2.17–2.68)	4.35±0.77 (4.05–4.86)	0.54±0.007 (0.50–0.57)	0.14±0.013 (0.04–0.17)	1.58±0.035 (1.45–1.79)	0.09±0.011 (0.02–0.12)	145.5±3.57 (129–153)	10.84±0.267 (10.02–11.48)	0.47±0.034 (0.41–0.62)	9.29±0.485 (7.88–10.78)
Elsothera genithecata												
Byangum AMC 152165 (Holotype)	1	4 1/4	2.77	5.63	0.49	—	1.65	—	153	8.64	—	—
AMC 153717	1	4 1/8	2.86	6.05	0.47	—	1.93	—	111	5.83	—	—
Red Scrub F.R. AMC 153718	1	4 5/8-	3.36	6.64	0.51	—	2.27	—	worn	—	—	—
Mt Warning QMMO 10484	1	4	2.77	4.37	0.63	—	1.09	—	worn	—	—	—

Elsothera sericatula (Pfeiffer, 1850)
(Figs 104–105; Tables 19, 21)

Helix sericatula Pfeiffer, 1850, p. 127; Reeve, 1852, pl. 132, sp. 812.

Elsothera sericatula (Pfeiffer); Iredale, 1933,p. 53; Iredale, 1937a, p. 324; Iredale, 1941a, p. 269, fig. 5.

COMPARISONS

A full treatment is deferred until a more comprehensive review of the genus is completed. *E. sericatula* resembles *E. nautilodea*, but differs in having the umbilicus closed (Fig. 104b) rather than slightly open (Fig. 106b). *'E.' biretracta* (Mousson, 1869) from the Illawarra region, NSW is conchologically similar to *E. sericatula* and may prove to be conspecific. Species of *Cralopa* are similar in having a closed umbilicus and prominent radial sculpture but are smaller with fewer, bolder ribs on the body whorl. The lectotype was selected from a lot of syntypes in the British Museum.

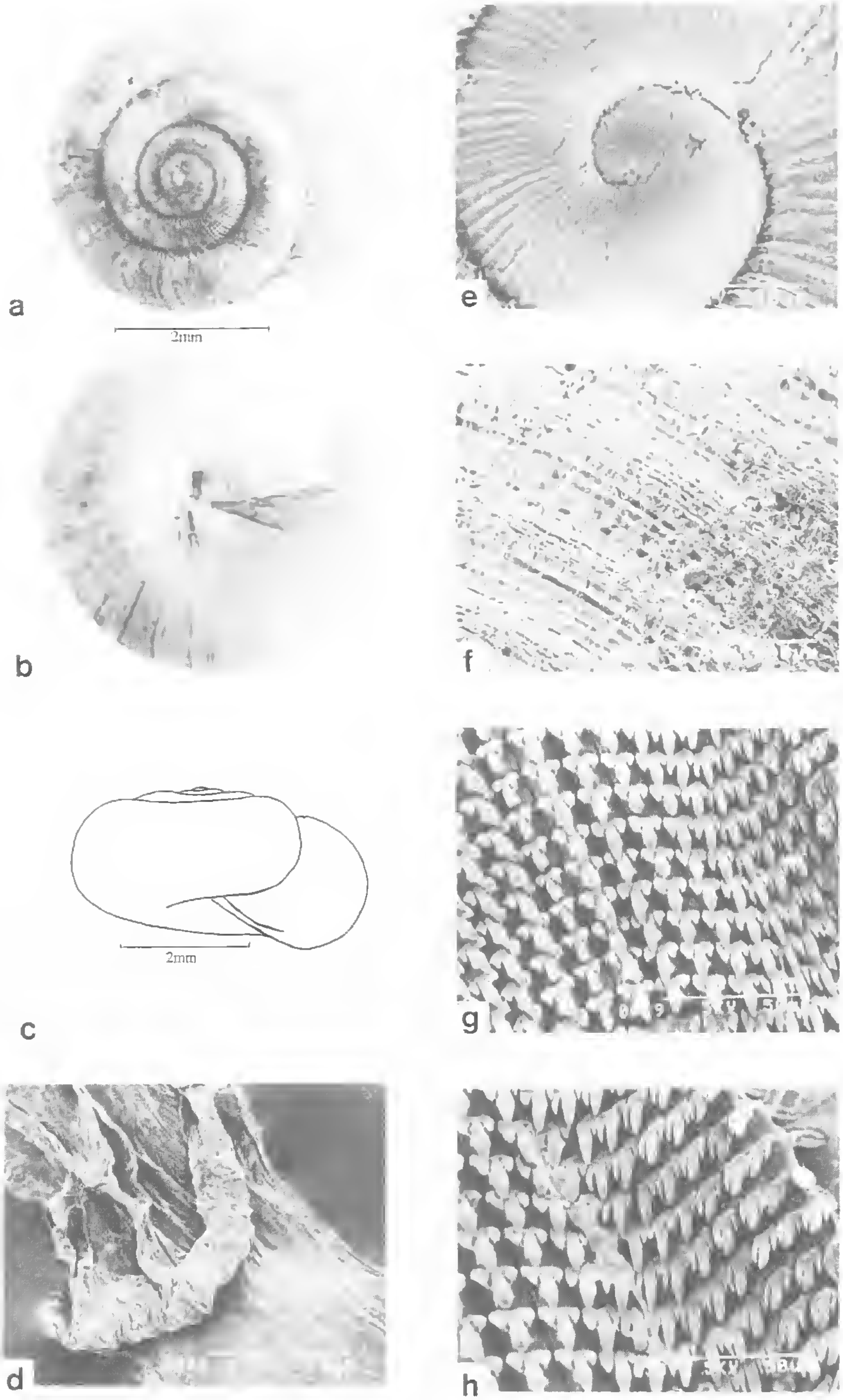
TYPE MATERIAL

LECTOTYPE: BMNH 1987055, Australia, H. Cuming Collection.

PARALECTOTYPES: BMNH 1987055, 3 specimens, same collection data as lectotype.

DESCRIPTION (of lectotype)

Shell small, diameter 4.64 mm, with 4 1/2 normally coiled whorls, the last descending more rapidly. Apex flat, spire slightly elevated, SP/BWW ratio 0.11, height 2.39 mm H/D ratio. Protoconch of 1 1/2 whorls, diameter 739 μm. Apical sculpture eroded with traces of radials near the sutures (paralectotypes show a pattern of high, slightly curved radials and low spirals). Post nuclear sculpture of numerous, closely spaced, prominent, protractively sinuated radial ribs, 190 on the body whorl. Ribs/mm 13.02. Microsculpture of fine radial riblets, 5–6 between each pair of major ribs, and low crowded spiral cords. Umbilicus closed by reflection of the columellar margin. Sutures impressed. Whorls shouldered above and rounded below a slightly laterally compressed periphery. Aperture ovately lunate. Lip simple, columellar margin slightly dilated reflected over the umbilicus. Parietal callus strongly developed. Colour light-grey with darker irregularly spaced radial markings.


a
2mm
b
2mm
c
d
e
f
g
h

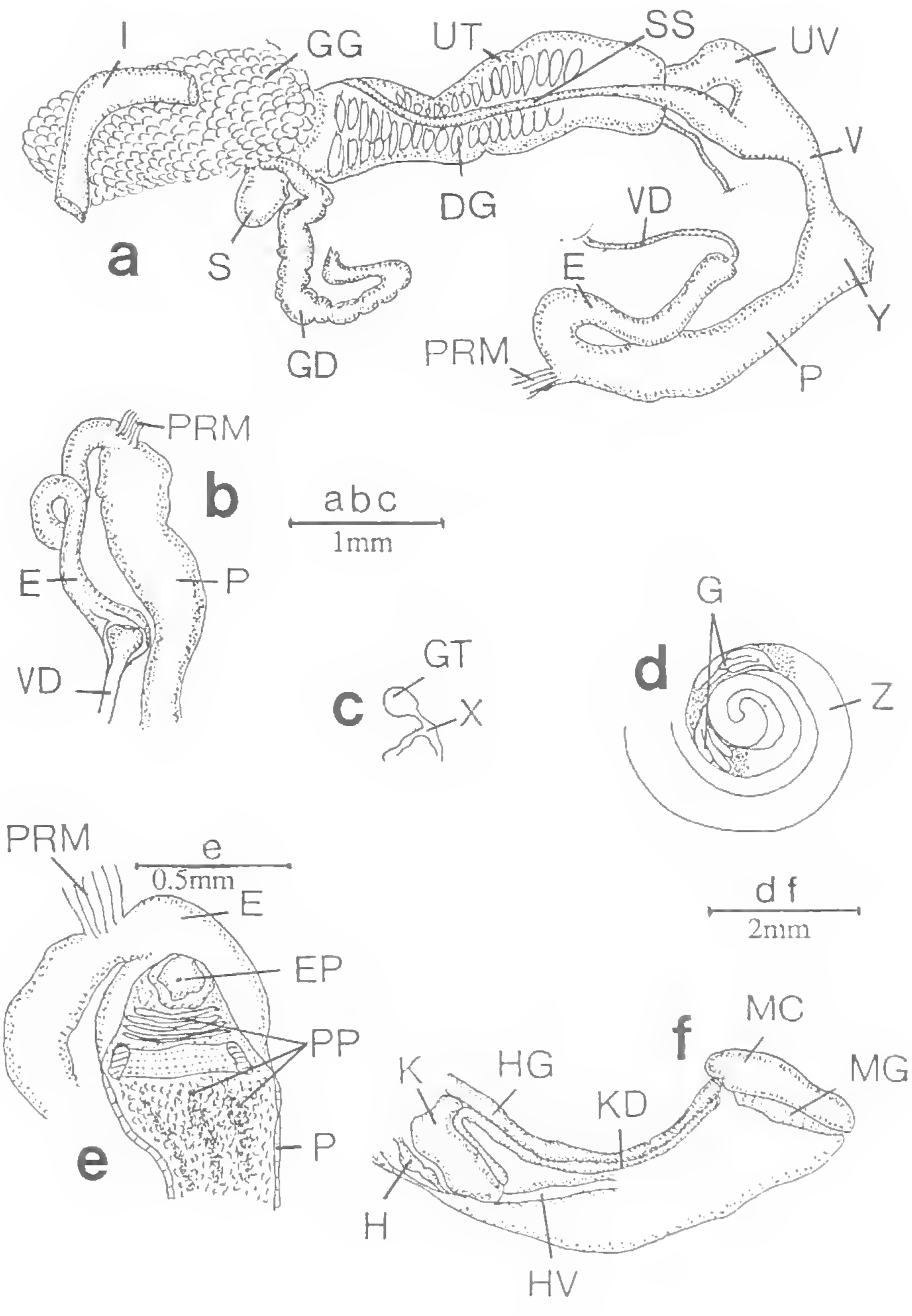


FIG. 105. *Elsothera sericatula* (Pfeiffer, 1850). Clive Park, Northbridge, NSW. AMC152205. a, genitalia; b, details of vas deferens - epiphallus junction; c, talon and carrefour; d, ovotestis; e, details of penis interior; f, pallial cavity. Scale lines as marked.

FIG. 104. *Elsothera sericatula* (Pfeiffer, 1850). a–c, Australia. BMNH 1987055, lectotype; c, g–h, Clive Park, Northbridge, NSW. AMC152205; e–f, Shark Is, Sydney, NSW. AMC103604. a–c, entire shell; d, jaw; e, apical sculpture; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale lines as marked.

OTHER MATERIAL STUDIED

Shark Is, Sydney NSW (13, AMC103604, ex J. Brazier coll); Clive Park, Northbridge, NSW, in fairly dense bush (3, AMC152205, 19 Oct 1969, W.F. Ponder, D.P. Fairfax).

ANATOMICAL DIAGNOSIS

Terminal male genitalia with a muscular epiphallus (Fig. 105a) which is partly coiled before entering the penis apically. Vas deferens/epiphallus junction (Fig. 105b) complex with vas deferens entering epiphallus laterally through a large cup-shaped pilaster. Penial retractor muscle inserting at the epiphallus/penis junction. Penis (Fig. 105e) short, tubular with an apical bulb, internally with a simple epiphallic entrance (Fig. 105e) and numerous short transverse pilasters. A large spongy collar constricts the entrance to the lower penial chamber which has fine spongy pustulations arranged in vague longitudinal rows (Fig. 105e). Vagina short with fleshy, pustular interior.

Radula (Fig. 104g,h) with tricuspid central and lateral teeth, central smaller.

Based on 2 dissected specimens (AMC-152205).

RANGE AND HABITAT

Closed and open forest from Cronulla to Gosford, NSW, extending westward to at least the Great Dividing Range. *E. sericatula* is a comparatively adaptable species and still survives in disturbed areas where microenvironments are suitable. It lives in the litter, among leaves and accummulated debris.

REMARKS

E. sericatula has been reported from Victoria (Gabriel, 1930) and Tasmania (Petterd and Hedley, 1909). However more recent surveys of these regional faunas (Smith and Kershaw, 1979, 1985) do not list this species and I regard the earlier records as erroneous.

Elsothera nautilodea (Cox, 1866) comb. nov.
(Figs 106–107; Tables 19, 21)

Helix nautilodea Cox, 1866a, p. 47.
Helix nautiloides Cox, 1866b, p. 696; non Ferussac, 1850.
Helix inusta Cox, 1868, p. 13, pl. 10, fig. 3.
Helix nautilodes (sic) Iredale, 1937a, p. 324.
Elsothera inusta (Cox); Iredale, 1937a, p. 324; Iredale, 1941a, p. 269.

COMPARISONS

E. nautilodea is conchologically similar to *E. sericatula*. However the species are allopatric and misidentification in the field is not likely. *E. nautilodea* has a brownish shell with very narrow umbilicus whereas the shell of *E. sericatula* is light grey with darker streaks and a completely closed umbilicus. *E. genithecata* is larger with relatively fewer whorls, more widely spaced ribs and channelled sutures (Fig. 108a). *Cralopa stroudensis* is smaller with fewer and bolder ribs.

PREVIOUS STUDIES

Helix nautilodea appeared on 1 January, 1866. In the same year, the same article appeared in the Proceedings of the Zoological Society (April 24, 1866) with the name changed to *H. nautiloides*. Subsequently Cox (1868) introduced *Helix inusta* as a replacement name for *H. nautiloides* after realising that the latter was preoccupied. I consider *nautilodea* to be the correct name for this species as there was never any indication by Cox that *H. nautiloides* was an emendation of the earlier name. The lectotype was chosen from topotypic material in the Cox collection.

TYPE MATERIAL

LECTOTYPE: AMC136903, Clarence River, NSW, ex Cox. Height of shell 2.81 mm, diameter 5.24 mm, H/D ratio 0.54, whorls 4 3/4-.

OTHER MATERIAL

Clarence Rv (2, AMC152170, ex C.F. McLauchlan); Grafton (2, AMC152171, Jan 1904, S.W. Jackson); Clarence Rv (6, AMC152172, G. Thornley); South Grafton (3, AMC152173, ex Nat. Mus. Vict.); Harwood Id, Clarence Rv (73, AMC152174, Feb 1961, A.A. Cameron); North Arm, Clarence Rv (9, AMC152212); on E side of tree 5 ft from ground Harwood Is, Clarence Rv, NSW (4, AMC152218, Jan 1970, A.A. Cameron).

DIAGNOSIS

Shell small, diameter 4.05–5.24 mm (mean 4.43 mm), of 4 1/4 to 4 3/4- (mean 4 3/8+) normally coiled whorls. Last whorl descending rapidly. Apex and spire (Fig. 106c) almost flat, SP/BWW ratio 0.02–0.12 (mean 0.09), height 2.17–2.81 mm (mean 2.41 mm). H/D ratio 0.50–0.57 (mean 0.54). Protoconch of 1 1/2 to 1 5/8 whorls, mean diameter 718.6 μm at 1 1/2 whorls. Apical sculpture (Fig. 106d) of curved radials and low, crowded spirals. Post nuclear sculpture (Fig. 106e) of numerous, closely spaced,

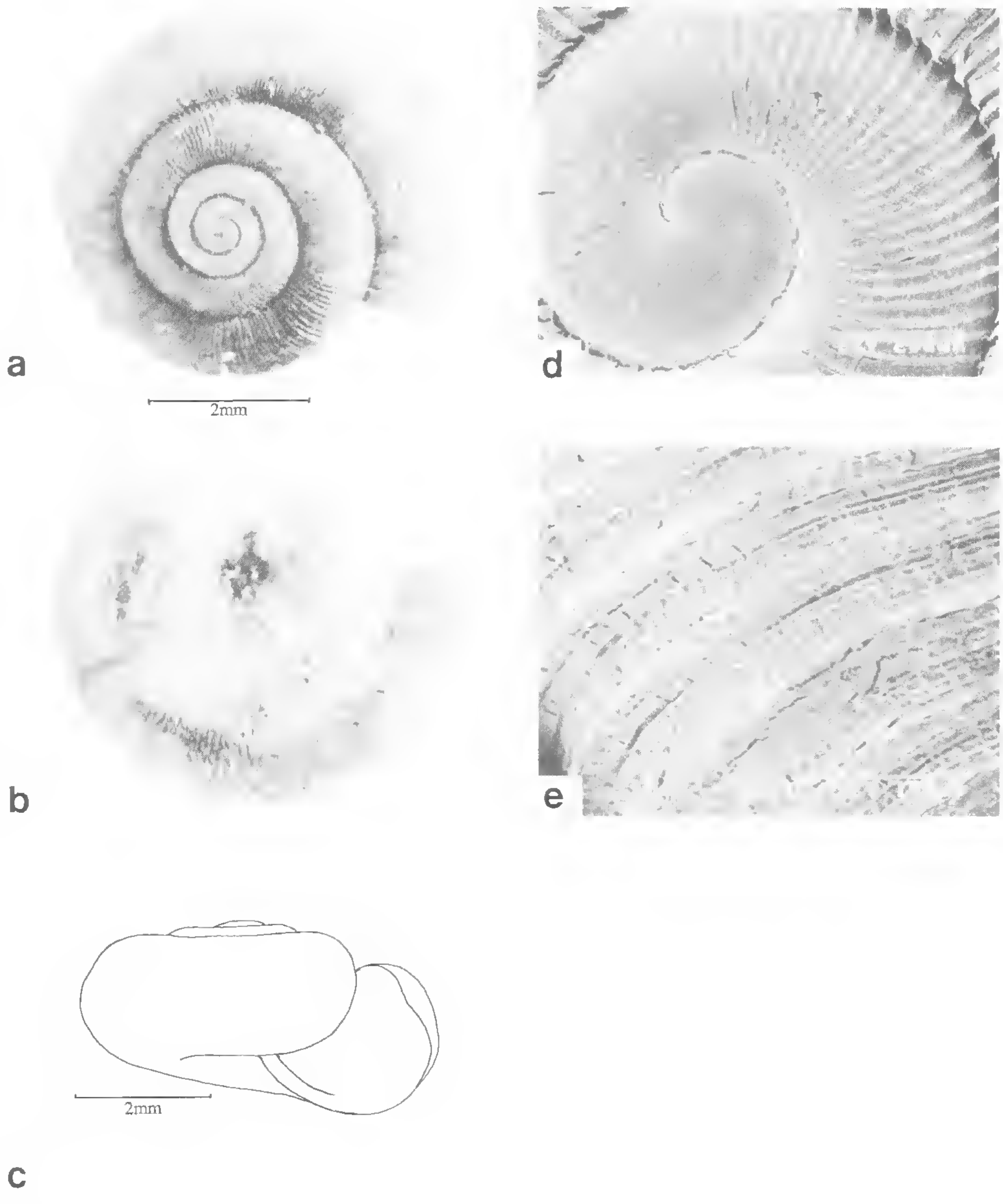


FIG. 106. *Elsothera nautilodea* (Cox, 1866). a–c, Clarence River, NSW. AMC136903, lectotype. d–e, Harwood Island, Clarence River, NSW. AMC152174. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture. Scale lines as marked.

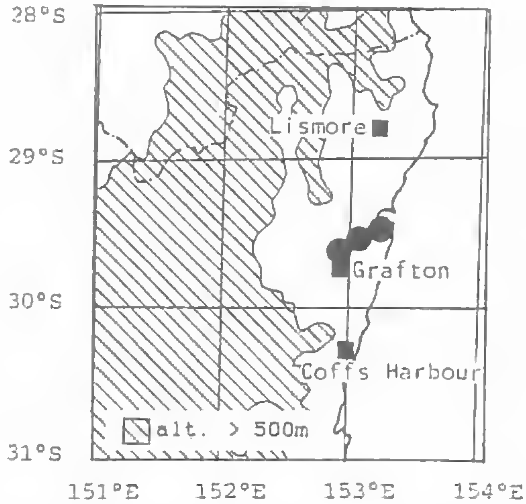


FIG. 107. Distribution of *Elsothera nautilodea* (Cox, 1866).

prominent, protractively sinuated radial ribs, 129–190 (mean 151.9) ribs on the body whorl. Ribs/mm 10.02–11.53 (mean 10.94). Microsculpture (Fig. 106e) of crowded spiral cords and thread-like radial riblets. 4–9 between each pair of major ribs. Umbilicus (Fig. 106b) a lateral crack to narrowly open, rarely completely closed. Sutures impressed. Whorls rounded below and strongly shouldered above a somewhat laterally compressed periphery with a weak subsutural sulcus formed in some specimens (Fig. 106e). Aperture roundly lunate. Lip simple, columella expanded and reflected over the umiblicus in some specimens. Parietal callus well developed. Colour brown with darker radial streaks. Based on 11 measured adults.

"Animal almost black, not quite, tentacles well defined and same colour as animal. Foot lighter in colour". (Based on field notes by A.A. Cameron, AMC152174). No soft parts available for dissection.

RANGE AND HABITAT

In spite of intensive collecting in northern NSW over six years, *E. nautilodea* has not been located. Earlier collections indicate the species on Harwood Island, at the mouth of the Clarence River. Live specimens have been taken semiarboreally.

Elsothera genithecata sp. nov.
(Figs 108–110; Tables 19, 21)

ETYMOLOGY

Latin *thecatus*, encased; referring to the sheathed epiphallus.

COMPARISONS

E. genithecata is not easily confused with sympatric charopids. Large size, small number of whorls, channelled sutures, well developed apertural sinus and closed umbilicus are not combined in other northern NSW charopids. *E. nautilodea* is smaller, has a less inflated body whorl and lacks sutural channelling. *Gyrocochlea* and *Nautiliropa* which have grossly similar adult sculpture, have a very depressed to sunken spire and wide U-shaped umbilicus.

TYPE MATERIAL

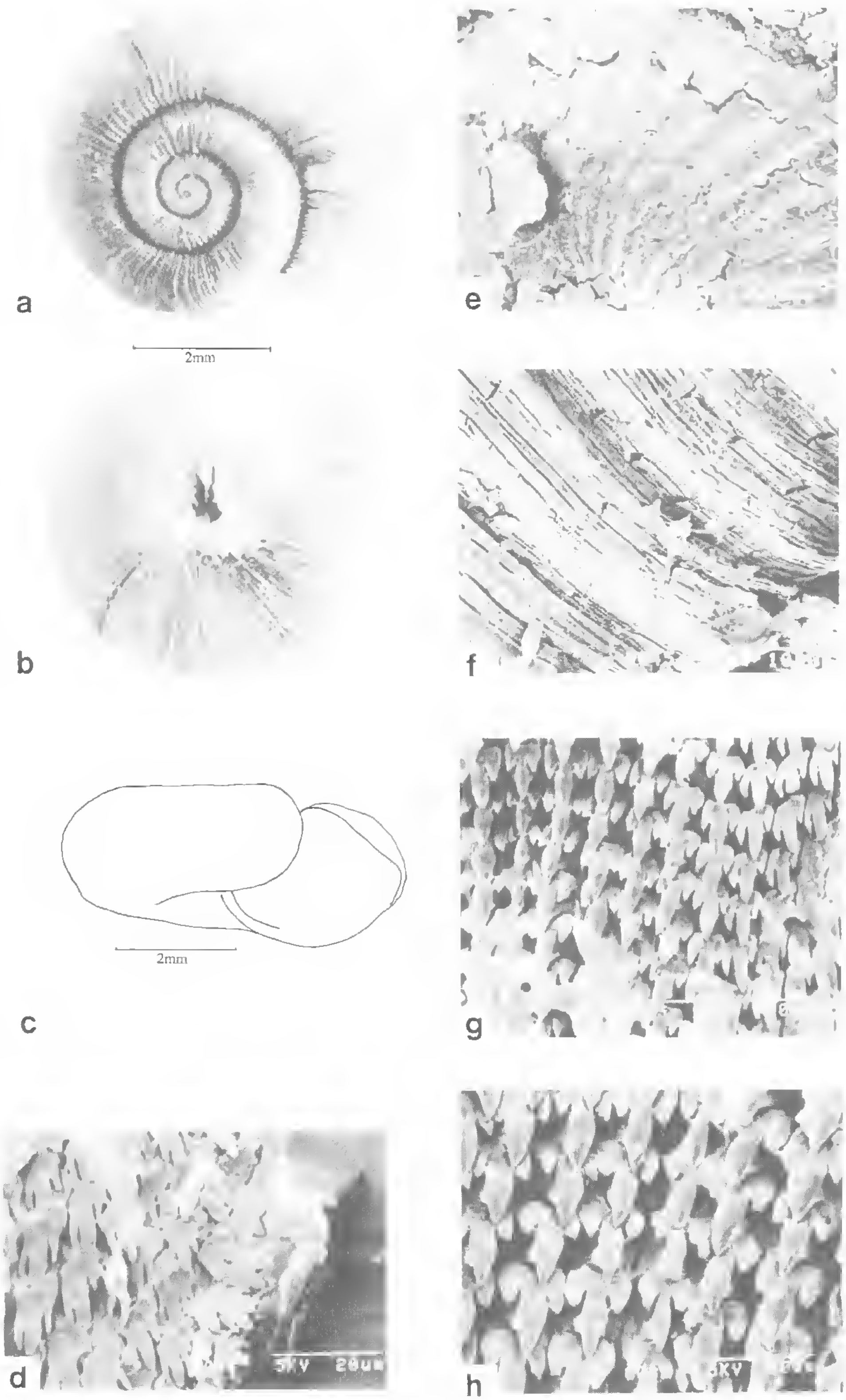
HOLOTYPE: AMC152165, Byangum, northern NSW, collected by Lower, ex Cox. Height of shell 2.77 mm, diameter 5.63 mm. H/D ratio 0.49, whorls 4 1/4.

PARATYPES: AMC153717, 2 specimens, same data as holotype; Red Scrub Flora Reserve, Whian Whian S.F., N of Lismore NSW (28°38'S, 153°19'E) 210 m, litter (2, AMC153718, 15 May 1976, P.H. Colman, I. Loch); Mt Warning N.P., NSW, near base, (28°24'S, 153°16'E) NVF/Palms (2, QMMO10484, QMMO-10502, 19 Mar 1981, AM/QM - ABRS); Richmond Range, S.F., NSW (28°39'S, 152°43'E) 400 m, open eucalypt forest (1, QMMO6267, 9 Apr 1976, M.J. Bishop); Big Scrub, Whian Whian S.F., N NSW (28°38'S, 153°19'30"E) SNVF, under logs (1, QMMO16772, 15 Nov 1983, AM/QM - ABRS); Mt Tamborine, SEQ, in floor litter in rainforest (AMC152164, 14 Sept 1979, P.H. Colman); Upper Tweed Rv, NSW (2, AMC152167, Petterd!, ex Cox); Emigrant Ck, Richmond Rv, NSW (4, AMC152168, ex Cox?); Byron Bay Scrubs, NSW (1, AMC152169, 1900, S.W. Jackson).

OTHER MATERIAL

Lower Ballanjui Falls Circuit, Binna Burra, Lamington N.P., SEQ, NVF, litter (1, QMMO16894, 30 Sept 1985, J. Stanisic, D. Potter, J. Chaseling);

FIG. 108. *Elosthera genithecata* sp. nov. a-c, Byangum, NSW, AMC152165, holotype; d, g-h, Richmond Range S.F., NSW, QMMO6267, paratype; e-f, Mt Warning N.P., NSW, QMMO10502, paratype. a-c, entire shell; d, marginal teeth; e, apical sculpture; f, post nuclear sculpture; g-h, central and lateral teeth. Scale lines as marked.


a
2mm
b
2mm
c
d
5KV 20um
e
f
g
h

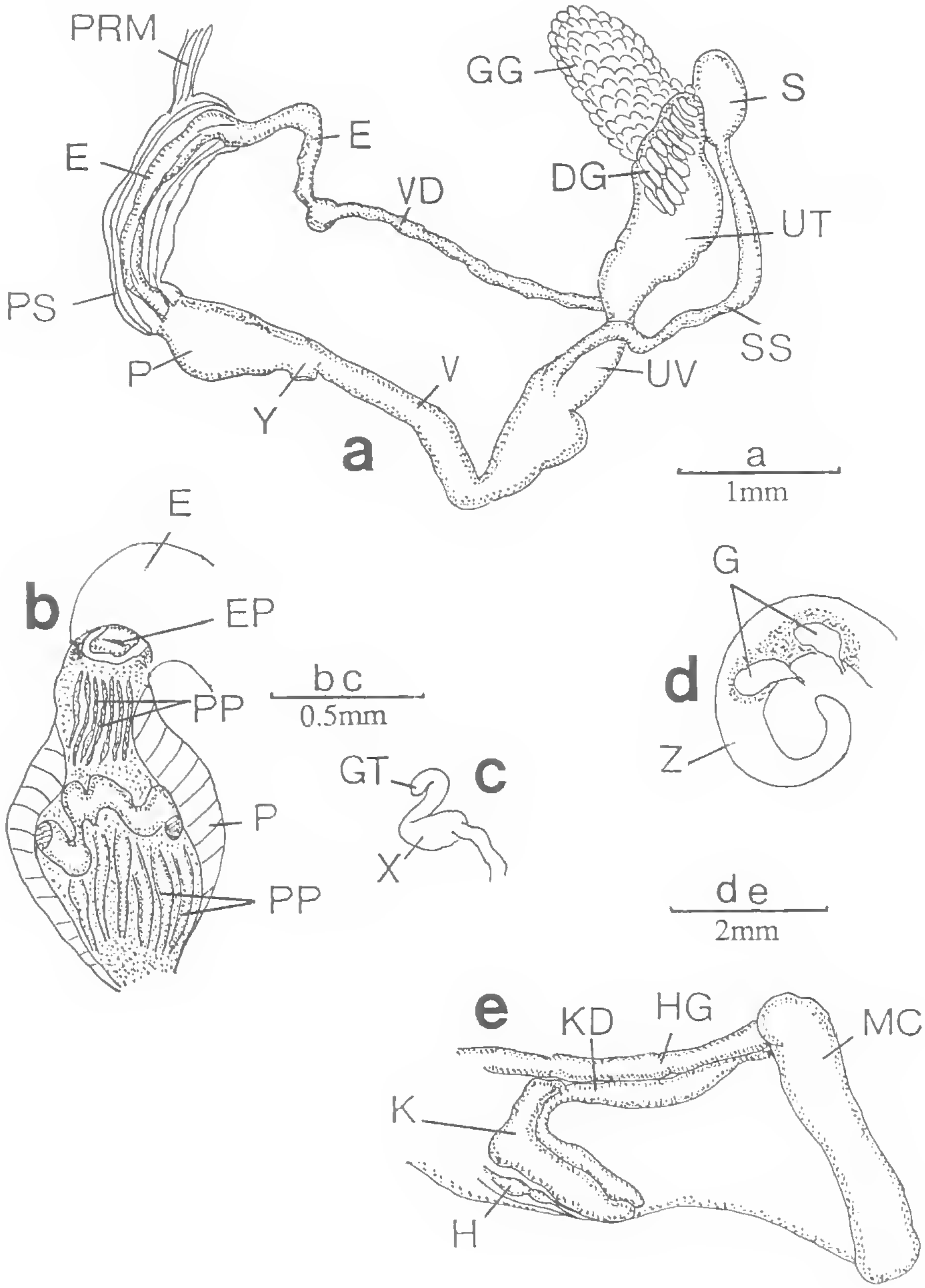


FIG. 109. *Elsothera genithecata* sp. nov. Big Scrub, Whian Whian S.F., NSW. QMMO16772, paratype. a, genitalia; b, penis interior; c, talon; d, ovotestis; e, pallial cavity. Scale lines as marked.

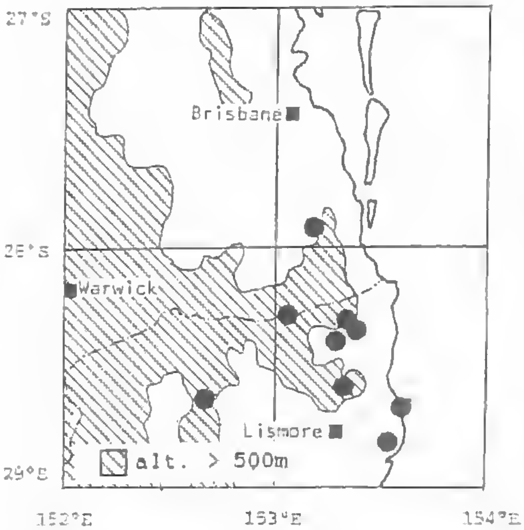


FIG. 110. Distribution of *Elsothera genithecata* sp. nov.

Clarence River, NSW (error!) (9, AMC103600, ex Cox).

DIAGNOSIS

Shell large, diameter 4.37–6.64 mm (mean 5.67 mm), with 4 to 4 5/8- (mean 4 1/4) loosely coiled whorls, the last whorl descending more rapidly and strongly inflated. Apex and spire flat, height 2.77–3.36 mm (mean 2.94 mm). H/D ratio 0.47–0.63 (mean 0.53). Protoconch of 1 1/2 whorls, mean diameter 821.3 μm. Apical sculpture (Fig. 108e) of high, slightly curved radial ribs, and low crowded spiral cords. Postnuclear sculpture (Fig. 108f) of numerous crowded, high, protractively sinuated radial ribs, 111–153 (mean 132) ribs on the body whorl. Ribs/mm 5.83–8.64 (mean 7.24). Microsculpture (Fig. 108f) of fine radial riblets, 5–10 between each pair of major ribs, and crowded spiral cords which continue onto the apices of the major radials. Umbilicus (Fig. 108b) closed or a very small lateral crack. Sutures deeply impressed. Whorls shouldered above and rounded below a slightly compressed periphery (Fig. 108c). Aperture roundly to ovately lunate. Lip sinuous, simple, retracted at the suture to form an apertural sinus (Fig. 108a-b). Columella vertical and thickened, reflected over the narrow umbilical opening. Parietal callus weakly developed. Colour light-brown with irregularly spaced dark radial streaks. Based on 4 measured adults.

Genitalia with vas deferens-epiphallus junction complex; vas deferens entering almost laterally through a large spongy pilaster (Fig. 109a). Epiphallus (Fig. 109a) long, convoluted with a large muscular sheath for the last half of its length, entering penis apically through a simple pore (Fig. 109b) surrounded by a circular collar. Penis (Fig. 109b) short, tubular with an apical bulb. Apical bulb internally with short, longitudinal pilasters and a transverse spongy collar constricting entrance to lower penial chamber. Lower penial chamber with numerous short longitudinal thickenings (Fig. 109b), and irregular pustulations nearer the atrium. Penial retractor muscle inserted on the epiphallic sheath. Vagina (Fig. 109a) long with a caecum containing a large internal spongy thickening, and an elongate basal extension.

Radula (Fig. 108d,g,h) with expanded mesocones on central and lateral teeth.

Based on 2 dissected specimens (AMC-152165, QMMO16772).

RANGE AND HABITAT

Warm moist subtropical notophyll vine forests of the Big Scrub area between the Richmond and Tweed Rivers, NSW; cooler subtropical forests of the Lamington Plateau, SEQ; palm dominated forest of Mt Tamborine, SEQ; and drier scrub of the Richmond Range, NSW. It lives under logs.

REMARKS

E. genithecata is one of the largest charopids in subtropical rainforests. The channelled sutures are an unusual development also seen in *Ngairea canaliculata* (Fig. 12a,c) and a number of extralimital taxa. The significance of this feature is not known. The well-developed apertural sinus is shared locally only with *Cralopa*, but is more common in New Zealand charopids.

Coenocharopa gen. nov.

ETYMOLOGY

Latin *coeno*, dirt; referring to adhering dirt particles on shell.

TYPE SPECIES

Coenocharopa sordidus sp. nov

DIAGNOSIS

Shell diameter 1.91-4.43 mm, with mean whorl count 4- to 4 3/8-. Whorls normally coiled, last descending.

Apex and spire slightly (*multiradiata, yessabahensis*) to conspicuously (*alata*) elevated. Apical sculpture of weak (*yessabahensis*) to prominent, curved radial ribs which may be crowded to moderately crowded (*alata*), more so at the nuclear-postnuclear junction, or regularly, widely spaced (*multiradiata*). Ribs with prominent periostracal blades. Secondary apical sculpture of crowded, squiggly spiral cords which are not continuous on the radials. Postnuclear sculpture of widely spaced (*alata*) to crowded (*yessabahensis*) weak radial ribs with prominent periostracal blades modified into wing-like processes in some species (*alata*), rarely lacking (*yessabahensis*). Microsculpture of thread-like radials which may have strongly developed periostracal blades (*multiradiata*) and low, broad (*alata*) to high, narrow (*multiradiata*) spiral cords. Dirt particles adhering to shell surface. Umbilicus narrow to moderately wide (*macromphala*), U-shaped. Sutures impressed, whorls strongly to weakly shouldered, occasionally with a supraperipheral sulcus (*macromphala*). Aperture roundly to ovately lunate. Lip simple, margins convergent. Parietal callus strongly developed.

Animal with foot and tail broad, bluntly tapered posteriorly. Terminal male genitalia with slender to expanded (*sordidus*) vas deferens. Epiphallus sometimes partially bound to penis sheath (*macromphala, alata*), entering penis apically through two fleshy thickenings. Penis large to very large (*sordidus*), tubular, with a sheath, internally with several longitudinal pilasters which are modified in some species (*sordidus, yessabahensis*). Penial retractor muscle inserted on or very near to the epiphallus/penis junction.

Radula with mesocone of the laterals greatly expanded in *C. yessabahensis*.

Distribution and Ecology

Warm temperate rainforests and thickets of the Yessabah-Carrai limestone outcrop, cool subtropical notophyll vine forests of the Great Dividing Range (from Dorrigo to the Border Ranges) and McPherson Ranges, and warmer subtropical notophyll vine forests (with *Araucaria*) in southern Queensland.

Intrageneric sympatry is complex when compared with other charopids examined in this study. Sympatric combinations are as follows: *C. sordidus/C. macromphala, C. sordidus/C. parvicostata, C. parvicostata/C. macromphala, C. alata/C. multiradiata, C. multiradiata/C. parvicostata, C. multiradiata/C. yessabahensis* and possibly *C. alata/C. parvicostata*. No details of microsympatry are available although this is likely in the case of *C. sordidus* and *C. macromphala*. *C. yessabahensis* has an enlarged penis and modified penial surface structures which indicate a microsympatric congener, probably *C. multiradiata*. Although sympatric with both *C. multiradiata* and *C. parvicostata*, *C. alata*, is probably not sympatric at the microhabitat level.

Patterns of Variation

Shell size and shape - Whorl counts correlate positively with increased size except in *C. multiradiata*. Spire protrusion is proportionately greatest in *C. alata*. Umbilical width is uniform except in *C. macromphala* where it is wider (Fig. 114c).

Shell Sculpture - The prominent calcified sculpture of most ground-dwelling charopids serves to lessen the chance of particle adherance.

Positive correlation between wider rib spacing and increased height of periostracal extension suggests that in *Coenocharopa* the periostracal elements may be compensating for the lack of primary rib sculpture. Nonetheless most species have their shells covered by a layer of adhering dirt particles. Reduced sculpture in *C. yessabahensis* correlates with living on rock surfaces where adherence of dirt particles may not be a major problem. *C. multiradiata* (Fig. 126d–f) most closely mimics the more typical sculpture as in *Rhophodon* and *Gyrocochlea*. Significantly it is the 'cleanest' species of *Coenocharopa*.

Genitalia - Variation in reproductive anatomy is confined to terminal male genitalia.

In *Ngairea, Gyrocochlea* and *Rhophodon* variation in penial surface among microsympaters involved minor changes in features of the apical chamber of the penis together with small changes in shape and size of the longitudinal pilasters. In contrast, alterations in *Coenocharopa* involve major shape changes in pilasters. The basic pattern of internal penial sculpture appears to be several longitudinal pilasters as in *C. macromphala* (Fig. 115d). *C. sordidus*, which is probably microsympatric with this species, has a large U-shaped pilaster and several accessory longitudinal thickenings (Fig. 112a).

Insertion of the penial retractor muscle displays only minor shifts from the penis/epiphallus junction onto the epiphallus adjacent to the junction. The epiphallus is typical, but in *C. macro-*

TABLE 22. RANGE OF VARIATION IN *COENOCHAROPA* AND *EGILOMEN* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Coenocharopa sordidula	7	4 3/8 (4+ to 4 5/8+)	2.31 (2.09–2.64)	3.92 (3.41–4.43)	0.59 (0.55–0.61)	0.34 (0.31–0.38)	1.36 (1.28–1.50)	0.26 (0.16–0.30)		--	1.11 (1.01–1.40)	3.56 (3.17–3.94)
Coenocharopa macromphala	11	4+ (3 3/4+ to 4 3/8–)	1.57 (1.28–1.83)	2.69 (2.17–2.98)	0.58 (0.52–0.64)	0.22 (0.13–0.30)	0.87 (0.77–0.94)	0.25 (0.15–0.33)	12	3.74	0.87 (0.70–1.13)	3.14 (2.64–3.54)
Coenocharopa alata	4	4– (3 3/4 to 4 1/4–)	1.49 (1.36–1.70)	2.49 (2.30–2.73)	0.60 (0.56–0.63)	0.28 (0.21–0.38)	0.75 (0.68–0.85)	0.37 (0.29–0.45)	–	--	0.60 (0.41–0.82)	4.38 (3.32–5.60)
Coenocharopa yessabahensis	20	4 3/8 (4 1/8–4 3/4)	1.88 (1.66–2.22)	3.40 (3.10–3.83)	0.55 (0.48–0.61)	0.23 (0.13–0.30)	1.16 (1.11–1.24)	0.20 (0.11–0.26)			0.83 (0.76–1.03)	4.12 (3.73–4.43)
Coenocharopa multiradiata	10	4– (3 7/8+ to 4 1/8+)	1.14 (1.07–1.19)	2.03 (1.91–2.16)	0.54 (0.53–0.62)	0.09 (0.06–0.12)	0.72 (0.66–0.74)	0.13 (0.08–0.16)	42.5 (38–47)	6.63 (5.78–6.96)	0.51 (0.47–0.55)	3.98 (3.79–4.36)
Coenocharopa parvicostata	17	4+ (3 3/4–4 3/8+)	1.31 (1.07–1.58)	2.36 (2.09–2.81)	0.57 (0.50–0.61)	0.17 (0.13–0.30)	0.82 (0.68–0.94)	0.21 (0.16–0.32)			0.57 (0.45–0.84)	4.16 (3.34–4.62)
Egilomen globosa	14	4 5/8+ (4 3/8–5)	1.64 (1.39–2.04)	2.14 (1.62–2.47)	0.77 (0.71–0.96)	0.34 (0.17–0.43)	0.80 (0.64–0.94)	0.43 (0.25–0.55)	64.1 (53–80)	9.01 (7.75–12.10)		--
Egilomen cochlidium	36	4 1/2+ (4– to 5 1/8–)	1.38 (0.95–1.63)	2.35 (1.91–3.07)	0.57 (0.49–0.61)	0.14 (0.06–0.27)	0.77 (0.58–0.98)	0.18 (0.09–0.27)	36.8 (30–47)	5.07 (4.22–5.90)	0.82 (0.60–1.03)	2.93 (2.50–3.47)

mphala and *C. alata* is partially bound to the penial sheath (Figs. 115a. 118b).

Radula - The enlarged mesocones of the central and lateral teeth of *C. yessabahensis* (Fig. 123d,h) resemble those in the sympatric *Letomola contortus* and *Rhophodon kempseyensis*.

COMPARISONS

Coenocharopa is distinct among genera reviewed in having a basically 'smooth' shell with strongly developed periostracal sculpture. Apical sculpture resembles *Elsothera* and *Cralopa* but these genera differ in having very prominent radial ribs on the postnuclear whorls, and closed or nearly closed umbilici. *Letomola* has greatly reduced sculpture but is much smaller, has modified apical sculpture, wide umbilicus and several apertural barriers (Figs 67, 68). In the Mudlo Gap area, north of Gympie, SEQ ,the conchologically similar *Lenwebbia* is sympatric with *Coenocharopa*. However, *Lenwebbia* is distinguished by its modified apical sculpture which consists of irregular pits and wrinkles (Fig. 29g), and postnuclear sculpture which includes incised spiral grooves (Fig. 29e). *Coenocharopa* shares some genital features with *Cralopa*. These include a tubular penis, simple epiphallic entrance into the penis through large fleshy thickenings, and basic penial surface sculpture of longitudinal pilasters (fewer in *Cralopa*) and background pustulations.

The postnuclear sculpture in *Coenocharopa* is deciduous and often lacking in older and dead specimens. The following key is based on new-adult fresh shells and may not work for gerontic or litter-retrieved specimens.

KEY TO SPECIES OF *COENOCHAROPA*

1. Shell with prominent wing-like periostracal processes (Fig. 117e,h); spire strongly elevated (Fig. 117c) .... *alata*

   Shell without prominent wing-like periostracal processes; spire weakly elevated 2

2. Apical sculpture of regularly spaced radial ribs, not crowded at the nuclear-postnuclear boundary (Fig. 126d) .... *multiradiata*

   Apical sculpture of curved radial ribs which become crowded at the nuclear-postnuclear boundary (Fig. 120f)................................... 3

3. Postnuclear sculpture of regular, widely spaced radial ribs with periostracal blades (Figs 111e, 114e, 120e) 4

Postnuclear sculpture of low, crowded radial ridges without prominent periostracal blades (Fig. 123e,g) .... *yessabahensis*

4. Shell larger, mean diameter 3.92 mm; apical sculpture of weak thread-like radials (Fig. 111f) .... *sordidus*

Shell smaller, mean diameter <3.00 mm; apical sculpture of low, prominent curved radial ridges (Figs 114f, 120f) 5

5. Umbilicus narrow, V-shaped, mean D/U ratio 4.16; shell colour glossy yellow-horn .... *parvicostata*

Umbilicus broader, V-shaped, mean D/U ratio 3.14; shell colour burnished-yellow or beige .... *macromphala*

Coenocharopa sordidus sp. nov.
(Figs 111–113; Tables 22, 23)

ETYMOLOGY
Latin *sordidus*, dirty; for the dirty shell.

COMPARISONS
C. sordidus is similar to *C. macromphala* but is distinguished by its larger size, narrower umbilicus (D/U ratio 3.56 compared with 3.14 for *C. macromphala*) and much finer sculpture. *C. sordidus* (Fig. 111f,g) has apical sculpture of vague radial ridges and crowded spiral cords extending onto post nuclear whorls, *C. macromphala* (Fig. 114 f,g) has prominent curved apical radial ribs and more widely spaced spiral cords on apex and post nuclear whorls. Anatomically *C. sordidus* is distinguished from *C. macromphala* by its larger terminal male genitalia which include a long epiphallus and vas deferens, and greatly expanded penis with modified pilaster pattern (Fig. 112a). *C. parvicostata* which is also sympatric with *C. sordidus*, has a more rounded, smaller shell, less elevated spire, smaller umbilicus and more prominently sculptured apex.

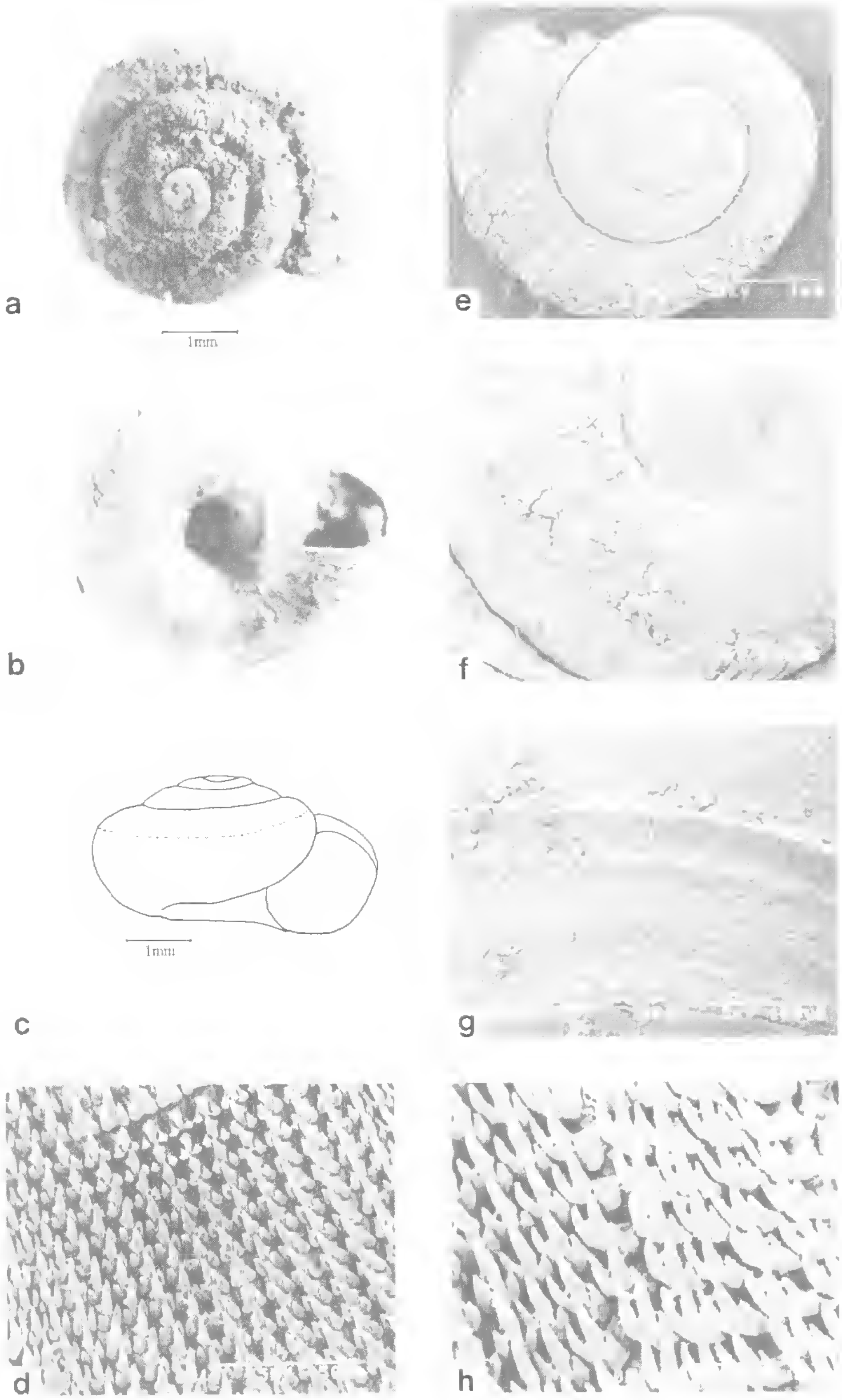
TYPE MATERIAL
HOLOTYPE: QMMO17276, Upper Brookfield, SEQ (27°30'S, 152°55'E) NVF/*Araucaria*, litter. Collected by V. Davies, R. Raven, 8 Apr 1981. Height 2.60 mm, diameter 4.43 mm, H/D ratio 0.59, D/U ratio 3.17, whorls 4 1/2+.
PARATYPES: SOUTH-EAST QUEENSLAND - QMMO11575, 8 specimens, same data as holotype; Freds Rd, Mt Mee (27°05'S, 152°43'E) rainforest, leaf litter (3, QMMO9696, 14 Apr 1980, J. Stanisic, A. Green, N. Hall); Dayboro - Mt Byron Rd, at crossing of North Pine River (27°15'S, 152°47'E) leaf litter (1, QMMO17277, 27 Apr 1980, J. Stanisic); Mt Guyra N.P. (25°49'S, 152°35'E) NVF/*Araucaria* (1, QMMO12073, 7 Sept 1982, AM/QM-ABRS); c. 1 km from Raynbird Creek Rd, on Lacey's Ck Rd, Laceys Creek, open scrub, litter (1, QMMO16834, J. Stanisic, G. Annabell, 2 Apr 1984); c. 11.3 km NE of Dandabah on Bunya Mts Rd (26°50'S, 151°33'E) (1, QMMO12303, 1 Sept 1982, AM/QM-ABRS); Upper Brookfield, NVF/*Araucaria*, litter (1, QMMO17271, 3 Mar 1981, V. Davies, R. Raven; 1, QMMO17268, 11 Dec 1980, V. Davies, R. Raven).

OTHER MATERIAL
Gold Creek Reserve, Upper Brookfield, SEQ, closed forest, litter (1, QMMO17278, 16 Dec 1980, V. Davies, R. Raven), Kenilworth S.F., SEQ (26°35'S, 152°42'E) NVF (2, QMMO6152, 18 May 1976, M.J. Bishop).

DIAGNOSIS
Shell small, often completely covered in dirt, depressed, diameter 3.41–4.43 mm (mean 3.92 mm) with 4+ to 4 5/8+ (mean 4 3/8-) normally coiled whorls. Apex and spire moderately elevated. SP/BWW ratio 0.16–0.30 (mean 0.26), height 2.09–2.64 mm (mean 2.31 mm). H/D ratio 0.55–0.61 (mean 0.59). Protoconch of 1 1/2 to 1 5/8 whorls, mean diameter 709.9 μm at 1 1/2 whorls. Apical sculpture (Fig. 111f) of weak, curved radial ribs becoming more crowded at the nuclear - postnuclear boundary, crossed by very crowded, weakly defined, squiggly spirals. Protoconch often appearing smooth in worn shells. Postnuclear sculpture (Fig. 111g) of strongly bladed, widely spaced, protractively sinuated radial ribs. Microsculpture (Fig. 111g) of thread-like radials and inconspicuous low spiral cords, which buttress both sides of the major radials. Sculpture continuous on the base. Umbilicus (Fig. 111b) narrow, U-shaped, diameter 1.01–1.40 mm (mean 1.11 mm), D/U ratio 3.17–3.94 (mean 3.56). Sutures impressed. Whorls shouldered above and slightly flattened below the periphery (Fig. 111c). Aperture roundly lunate, margins convergent. Lip simple. Columella slightly dilated. Parietal callus prominent, uniting lip margins. Colour

TABLE 23 - LOCAL VARIATION IN *COENOCHAROPA SORDIDUS* SP. NOV., *COENOCHAROPA MACROMPHALA* SP. NOV. AND *COENOCHAROPA ALATA* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Coenocharopa sordidus												
Brookfield												
QMMO 17276 (Holotype)	1	4 1/2+	2.60	4.43	0.59	0.38	1.45	0.27	---	---	1.40	3.17
QMMO 11575	2	4 1/2- (4 1/4–4 5/8+)	2.43±0.210 (2.22–2.64)	4.24±0.190 (4.05–4.43)	0.58±0.025 (0.55–0.60)	0.38	1.43±0.105 (1.32–1.53)	0.27±0.020 (0.25–0.29)	---	---	1.13±0.100 (1.03–1.23)	3.77±0.175 (3.59–3.94)
Dayboro												
QMMO 17277	1	4+	2.22	3.83	0.58	0.21	1.32	0.16	---	---	1.03	3.73
Laceys Ck												
QMMO 16834	1	4 3/8	2.17	3.66	0.59	0.38	1.28	0.30	---	---	1.01	3.64
NE of Dandabah												
QMMO 12303	1	4 3/8	2.22	3.62	0.61	0.38	1.32	0.29	---	---	1.03	3.52
Mt Guyra												
QMMO 12073	1	4 1/4-	2.09	3.41	0.61	0.30	1.28	0.23	---	---	1.03	3.32
Coenocharopa macromphala												
Brookfield												
QMMO 17263 (Holotype)	1	4 3/8-	1.83	2.98	0.61	0.30	0.94	0.32	---	---	1.13	2.64
QMMO 11576	2	4 (4–4+)	1.55±0.022 (1.53–1.58)	2.75±0.021 (2.73–2.77)	0.57±0.005 (0.56–0.57)	0.21±0.043 (0.17–0.26)	0.83±0.064 (0.77–0.89)	0.26±0.070 (0.19–0.33)	---	---	0.87–0.011 (0.86–0.88)	3.15–0.015 (3.13–3.16)
Blackbutt Ra												
QMMO 16828	6	3 7/8+ (3 3/4–to4 1/8)	1.46±0.063 (1.28–1.70)	2.59±0.047 (2.47–2.73)	0.57±0.015 (0.52–0.63)	0.19±0.027 (0.13–0.30)	0.87±0.018 (0.81–0.94)	0.22±0.028 (0.15–0.33)	32	3.74	0.78±0.019 (0.70–0.82)	3.31±0.060 (3.11–3.54)
QMMO 12241	2	4 1/4 (4 1/8+to4 3/8-)	1.75±0.043 (1.70–1.79)	2.79±0.107 (2.68–2.90)	0.63±0.010 (0.62–0.64)	0.26	0.89±0.043 (0.85–0.94)	0.29±0.015 (0.27±0.30)	---	---	0.99±0.103 (0.88–1.09)	2.82±0.220 (2.66–3.04)
Coenocharopa alata												
Koreelah S.F.												
QMMO 17279 (Holotype)	1	4 1/4-	1.70	2.73	0.63	0.38	0.85	0.45	---	---	0.82	3.32
QMMO 10961	1	3 7/8	1.41	2.43	0.58	0.21	0.72	0.29	---	---	0.58	4.22
Binna Burra												
QMMO 6210	1	3 3/4-	1.36	2.30	0.59	0.26	0.68	0.38	---	---	0.41	5.60


a
1mm
e
b
f
1mm
c
g
d
h

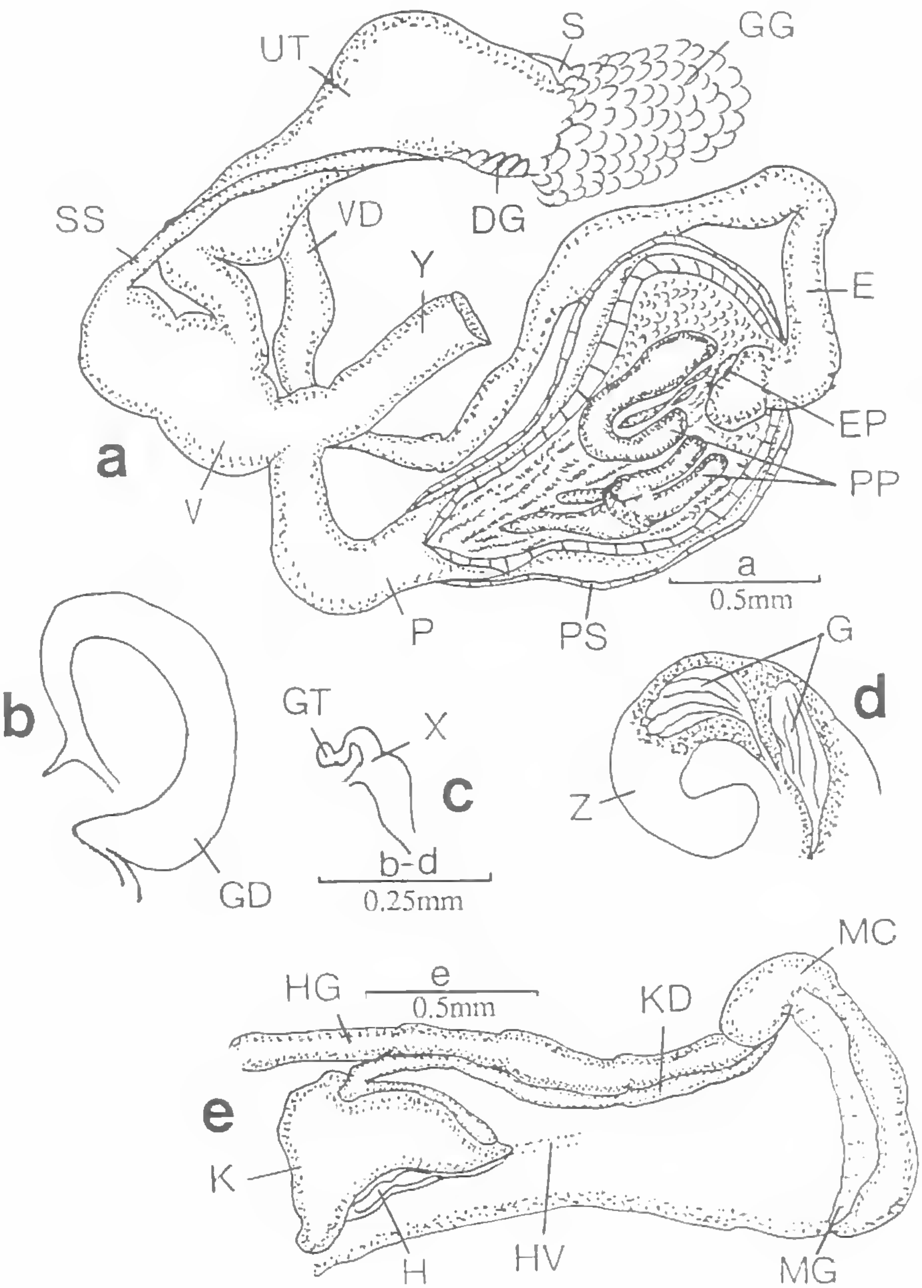


FIG. 112. *Coenocharopa sordidus* sp. nov. Upper Brookfield, SEQ. QMMO17268, paratype. a, genitalia and details of penis interior; b, hermaphroditic duct; c, talon and carrefour; d, ovotestis; e, pallial cavity.

FIG. 111. *Coenocharopa sordidus* sp. nov. a–c, Upper Brookfield, SEQ. QMMO17276, holotype; e–g, Fred's Rd, Mt Mee, SEQ. QMMO9696, paratype; d, h, Upper Brookfield, SEQ. QMMO17271, paratype. a–c, entire shell; d, central and lateral teeth; e, entire shell; f, apical sculpture; g, post nuclear sculpture; h, lateromarginal teeth. Scale lines as marked.

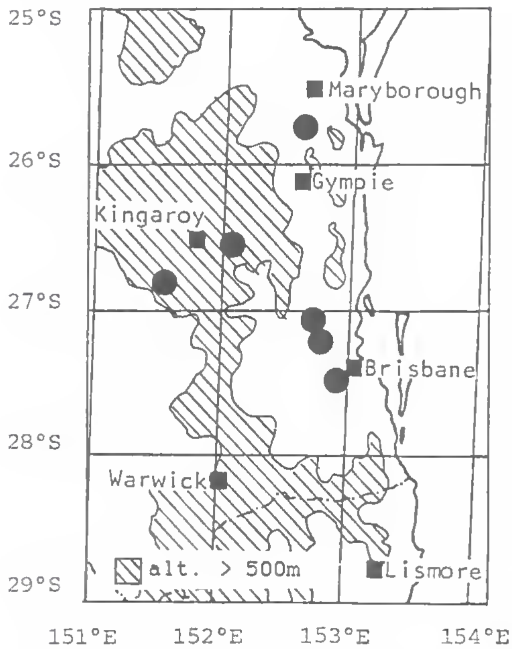


FIG. 113. Distribution of *Coenocharopa sordidus* sp. nov.

dirty yellow-horn when clean. Based on 7 measured adults.

Vas deferens (Fig. 112a) large, convoluted, giving rise to a more expanded, muscular epiphallus which is as long as the penis. Epiphallus (Fig. 112a) entering penis apically through a spongy pilaster. Penial retractor muscle inserted at the penis-epiphallus junction. Penis (Fig. 112a) with an enlarged upper chamber receiving the epiphallus and enveloped in a thin sheath; internally (Fig. 112a) with a very large spongy horseshoe-shaped pilaster opposite the epiphallic pore, and a series of short longitudinal thickenings below. Lower chamber with irregular spongy pustules arranged in vague longitudinal rows.

Radula (Fig. 111d,h) without unusual features. Based on 3 dissected specimens (QMMO-17268, QMMO17278, QMMO17271).

Range and Habitat

Drier araucarian vine forests between Brookfield, Mt Guyra, and the Bunya Mountains, SEQ. It has been caught in pitfall traps set for ground dwelling spiders and probably lives among friable soil and litter. *C. sordidus* has been collected in degraded forest at Laceys Creek and along the Dayboro-Mt Byron Road, SEQ. These are areas with little rainforest that have been largely cleared for farming.

Remarks

C. sordidus is identified by its size and almost completely dirt-encrusted shell (Fig. 111a). It is inconspicuous in the field.

Coenocharopa macromphala sp. nov.
(Figs. 114–116; Tables 22, 23)

Etymology

Latin *macro-*, large; Greek *omphalos*, umbilicus; referring to large umbilicus.

Comparisons

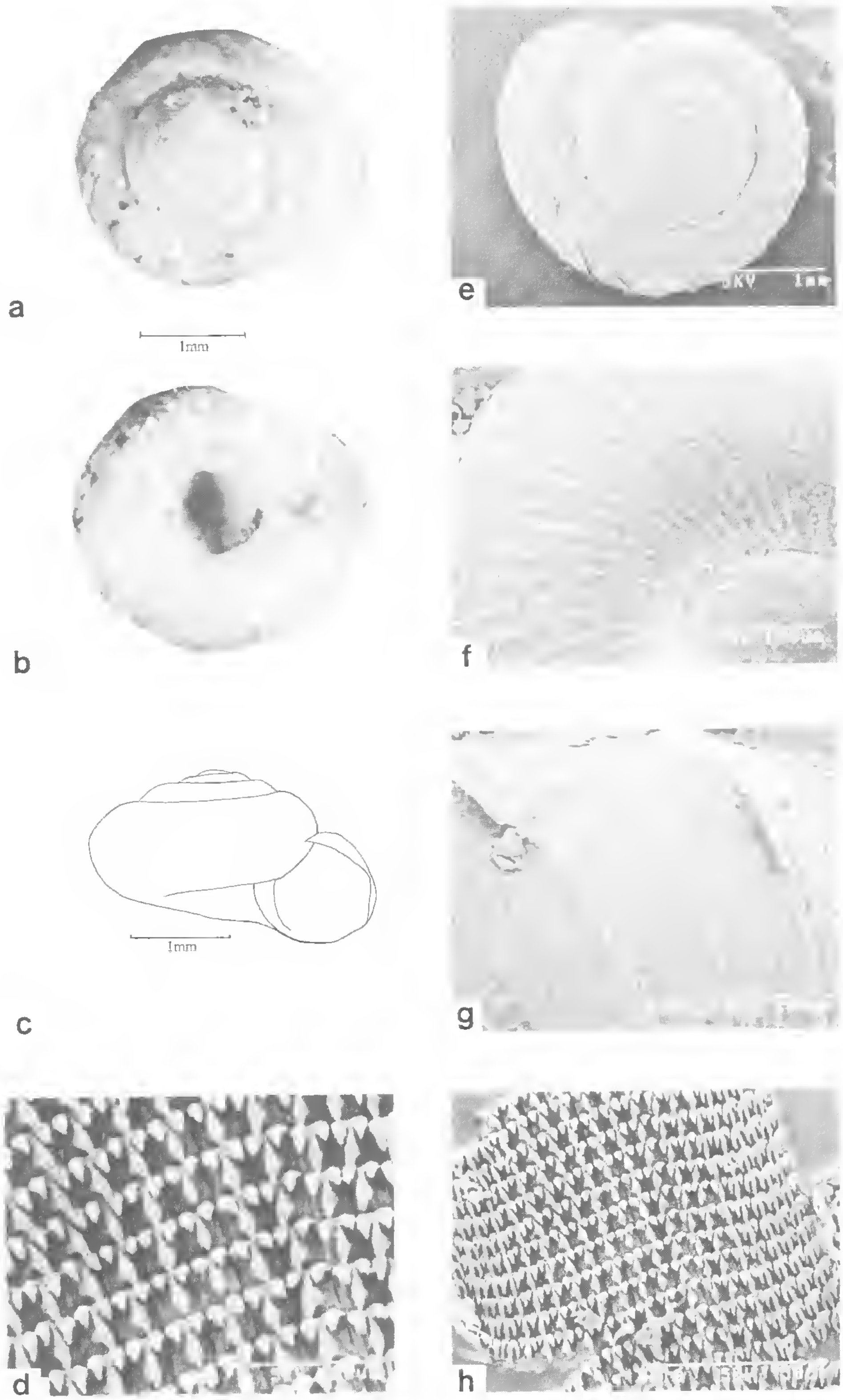
C. macromphala may be confused with *C. sordidus* but the wider umbilicus, smaller shell, more prominent apical sculpture and more widely spaced spiral cords on the postnuclear whorls, distinguish it from that species. *C. parvicostata* (Fig. 120a–c) has more rounded shell whorls, flatter spire and much smaller umbilicus. *Lenwebbia protoscrobiculata* is sympatric in the Mt Mudlo area, north of Gympie, SEQ. It has apical sculpture of irregular pits and wrinkles, and postnuclear sculpture that includes incised spiral grooves (Fig. 29e,g).

Type Material

Holotype: QMMO17263, Upper Brookfield, SEQ (27°30'S, 152°55'E), litter, NVF/*Araucaria*. Collected by V. Davies, R. Raven, 8 Apr 1981. Height of shell 1.83 mm, diameter 2.98 mm, H/D ratio 0.61, D/U ratio 2.64, whorls 4 3/8-.

Paratypes: SOUTH-EAST QUEENSLAND - QMMO11576, same data as holotype: Upper Brookfield, CNVF/*Araucaria* (2, QMMO17262, 3 Mar 1981, V. Davies, R. Raven); beside Bruce Hwy, Blackbutt Range, under logs, NVF/*Araucaria* (8, QMMO16828, 12 May 1984, J. Stanisic, D. Potter); c. 7.4 km S of Benarkin, Blackbutt Range (26°53'S, 152°11'E) (12, QMMO12241, AMC136567, 31 Sept 1982, AM/QM-ABRS); Upper Brookfield, NVF/*Araucaria*, litter (2, QMMO17265, 28 Nov. 1980, V. Davies, R. Raven); Mt Mudlo, Kilkivan S.F., (26°01'S, 152°13'E),

FIG. 114. *Coenocharopa macromphala* sp. nov. a–c, Upper Brookfield, SEQ. QMMO17263, holotype. d–h, same data as holotype. QMMO17265, QMMO11576, paratypes. a–c, entire shell; d, central and lateral teeth; e, entire shell; f, apical sculpture; g, post nuclear sculpture; h, radula. Scale lines as marked.


a
1mm
b
c
1mm
d
e
1mm
f
g
h

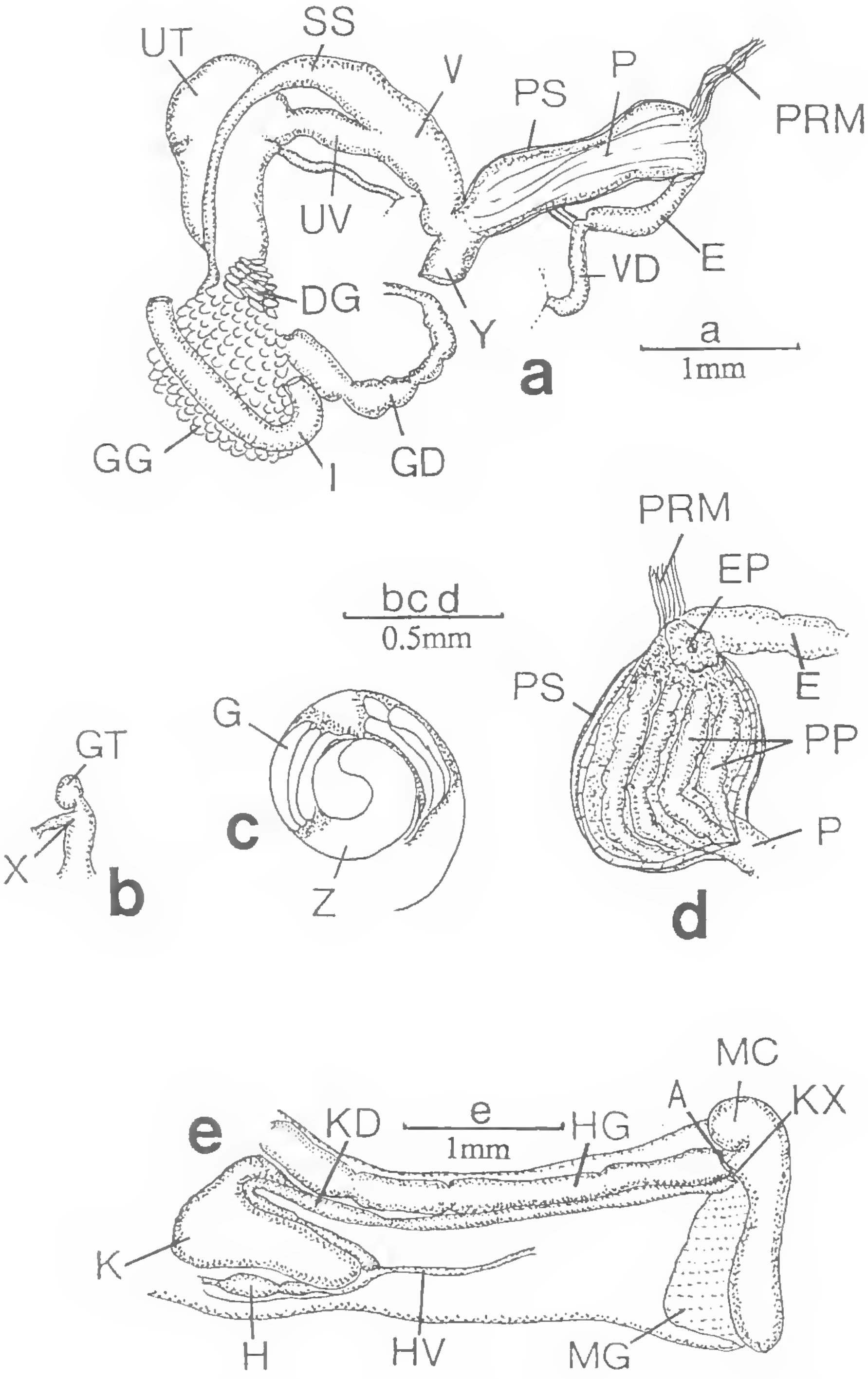


FIG. 115. *Coenocharopa macromphala* sp. nov. Beside Bruce Hwy, Blackbutt Range, SEQ. QMMO16828, paratype. a, genitalia; b, talon and carrefour; c, ovotestis; d, details of penis interior; e, pallial cavity. Scale lines as marked.

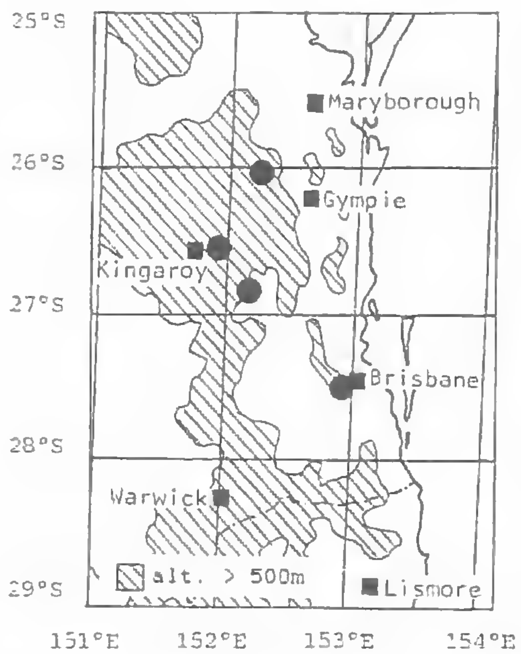


FIG. 116. Distribution of *Coenocharopa macromphala* sp. nov.

NVF/*Araucaria*, leaf litter (4, QMMO18974, 17 Jul 1980, J. Stanisic, A. Green).

OTHER MATERIAL

Coolabunia Pine Scrubs, Kingaroy, SEQ (1, AMC32999, Jun 1908, S.W. Jackson).

DIAGNOSIS

Shell small, depressed, diameter 2.47–2.98 mm (mean 2.69 mm) with 3 3/4- to 4 3/8- (mean 4+) loosely coiled whorls, last descending more rapidly. Apex and spire (Fig. 114c) moderately elevated, SP/BWW ratio 0.15–0.33 (mean 0.25), height 1.28–1.83 mm (mean 1.57 mm). H/D ratio 0.52–0.64 (mean 0.58). Protoconch of 1 3/8 to 1 1/2- whorls, mean diameter 647.8 µm at 1 1/2 whorls. Apical sculpture (Fig. 111f) of crowded, protractively sinuated radial ribs which become more crowded at the nuclear-postnuclear boundary, crossed by fine spiral cords. Postnuclear (Fig. 114g) sculpture of irregularly spaced, protractively sinuated radial ribs with conspicuous periostracal blades that are often worn, 20–30 ribs on the body whorl. Microsculpture (Fig. 114g) of numerous low thread-like curved radial riblets and low crowded spiral cords. Umbilicus (Fig. 114b) broadly V-shaped, diameter 0.70–1.13 mm (mean 0.87 mm), D/U ratio 2.64–3.54 (mean 3.14). Sutures strongly impressed. Whorls (Fig. 114c) rounded above and below the periphery, with a supra-peripheral sulcus. Aperture roundly to ovately lunate. Lip simple, columella dilated and slightly twisted toward the umbilicus. Parietal callus strongly developed and connecting lip margins. Colour burnished yellowy-beige. Based on 11 measured adults.

Genitalia with large, muscularised epiphallus (Fig. 115a); internally with longitudinal thickenings and entering the penis apically through a simple pore. Epiphallus partially bound to the penis sheath by short fibres. Penis (Fig. 115d) tubular, internally with low pustules in the apical portion giving rise to low, spongy, longitudinal thickenings in the penis proper. Penis sheath present. Penial retractor muscle long, inserting at the epiphallus/penis junction. Vagina muscular with low pustules internally.

Radula (Fig. 114d,h) similar to that of *C. sordidus*.

Based on 3 dissected specimens (QMMO-16878, QMMO17265).

RANGE AND HABITAT

Prefers drier araucarian notophyll vine forests between Brookfield and Mt Mudlo, SEQ. Like *C. sordidus*, *C. macromphala* has been collected in pitfall traps and probably lives in friable earth and litter. Distribution is poorly known.

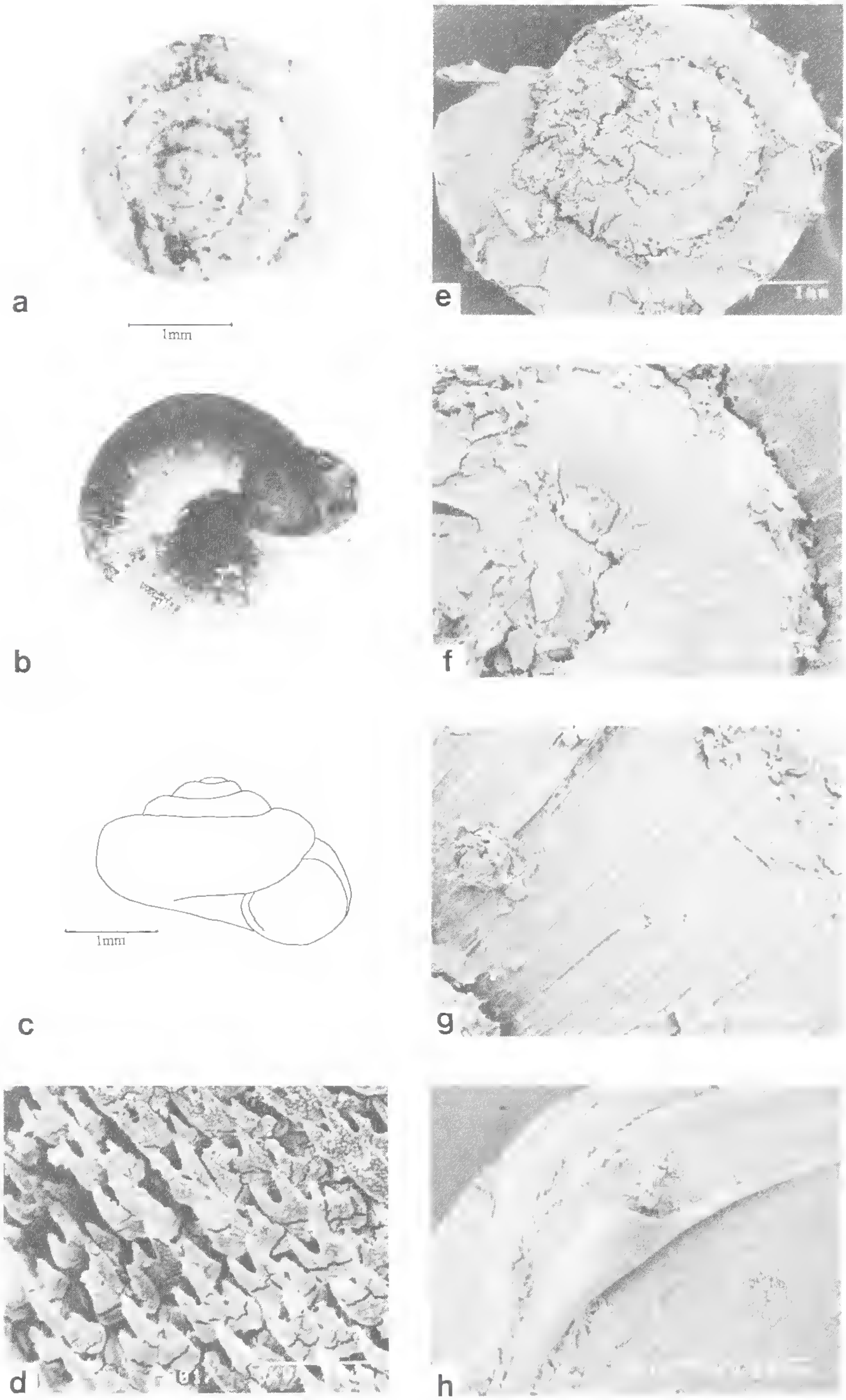
Coenocharopa alata sp. nov.
(Figs 117–119; Tables 22, 23)

ETYMOLOGY

Latin *alatus*, a wing; refers to wing-like periostracal processes.

COMPARISONS

Live specimens are recognised by their large wing-like periostracal extensions (Fig. 117e,h) which are deciduous and often lost in dead specimens. Worn shells can be distinguished from *C. macromphala* by their comparatively higher spire and smaller umbilicus; from *C. parvicostata* by their strongly elevated spire and flatter periphery; and from *C. multiradiata* by their larger size and less regular sculpture. *C. alata* has a more immediate resemblance to some species of the punctid genus *Paralaoma* Iredale, 1913. That genus is much smaller and has apical sculpture of low, rounded spiral cords.


a
1mm
e
b
f
1mm
c
g
d
h

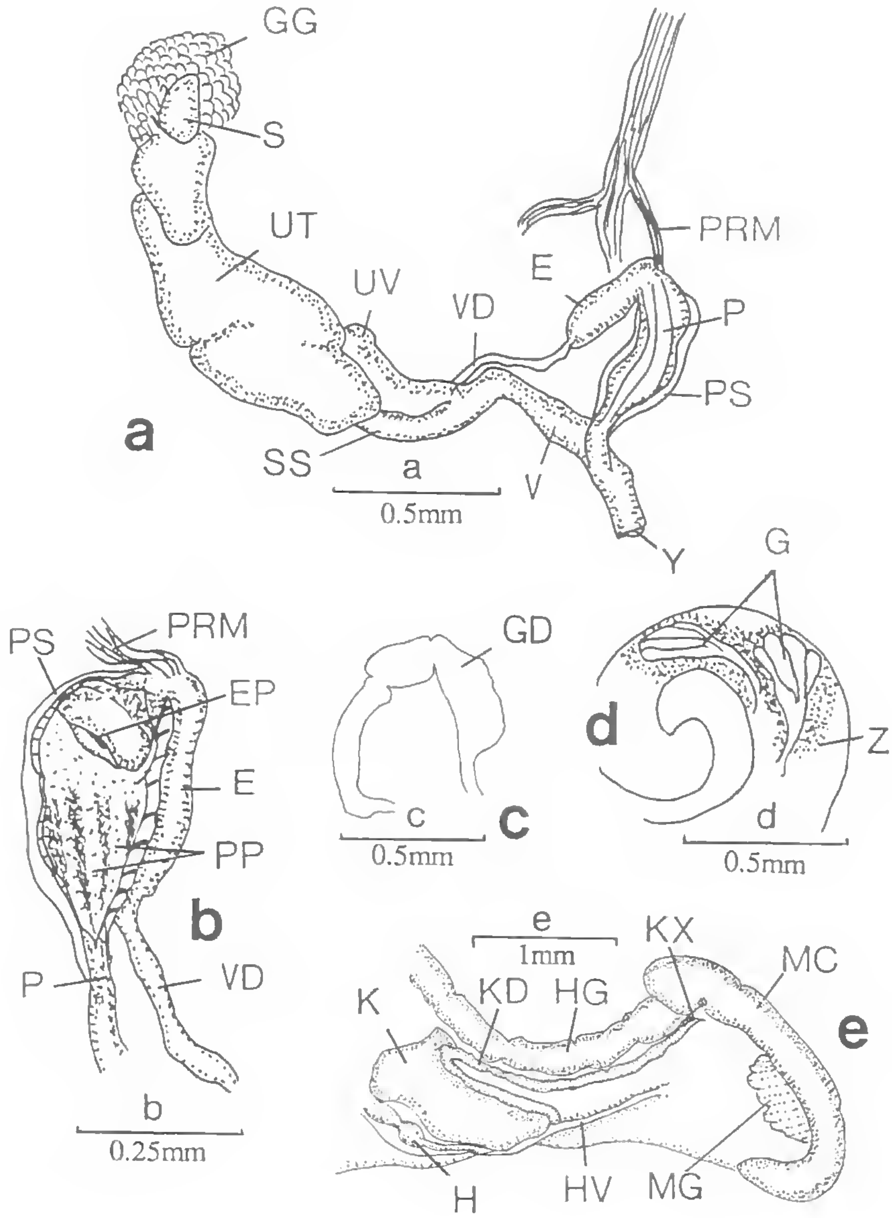


FIG. 118. *Coenocharopa alata* sp. nov. a, c, 12.2km from Acacia Plateau-Killarney Rd, Koreelah S.F., NSW. AMC128563, paratype. b–e, Coombadjha Walk, Washpool N.P., Gibralter Range, NSW. QMMO17270, paratype. a, genitalia; b, details of penis interior; c, hermaphroditic duct; d, ovotestis; e, pallial cavity. Scale lines as marked.

FIG. 117. *Coenocharopa alata* sp. nov. a–c, c. 12.2km from Acacia Plateau-Killarney Rd, Koreelah S.F., NSW. QMMO17279, holotype; d, same data as holotype. QMMO10961, paratype; e-g, Wiangarie S.F., c. 24km N of Kyogle, NSW. AMC150094, paratype; h, Gibralter Range, NSW. QMMO17270, paratype. a–c, entire shell; d, lateromarginal teeth; e, entire shell; f, apical sculpture; g, post nuclear sculpture; h, details of periostracal process. Scale lines as marked.

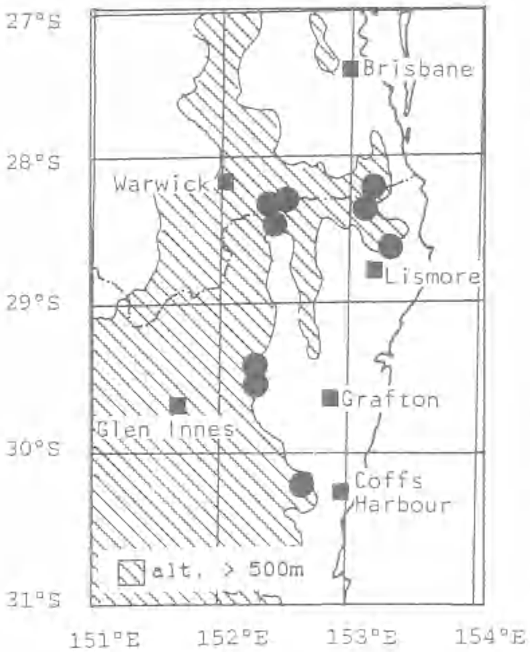


FIG. 119. Distribution of *Coenocharopa alata* sp. nov.

TYPE MATERIAL

HOLOTYPE: QMMO17279, c. 12.2 km from Acacia Plateau - Killarney Rd, Koreelah S.F., NENSW, 850 m, SEVT/Araucaria. Collected 15 Mar 1981, AM/QM-ABRS. Height of shell 1.70 mm, diameter 2.73 mm, H/D ratio 0.63, D/U ratio 3.32, whorls 4 1/4-.

PARATYPES: QMMO10961, AMC128563, 21 specimens, same data as holotype; Binna Burra, Lamington N.P., SEQ, 850 m, CNVF (28°13'S, 153°12'E) (1, QMMO6210, Apr 1976, M.J. Bishop); Wiangarie S.F., c. 25 km NE of Kyogle, NENSW, 1000 m (28°23'S, 153°06'E) litter (6, AMC150094, 17 May 1976, P.H. Colman, I. Loch); Moonpar S.F., NENSW, 0.6 km along Mills Rd from Moonpar Rd intersection, NSW (30°13'S, 152°39'E), under moss on log (1, QMMO17269, 7 Mar 1987, J. Stanisic, D. Potter); Coombadjha Walk, Washpool N.P., Gibralter Range, NSW (29°28'S, 152°16'E) (1, QMMO17270, 8 Mar 1987, J. Stanisic, D. Potter); Gibralter Range, N.P., NENSW, rainforest (1, QMMO17289, G. Monteith, 10 Nov 1980). Beaury S.F., c. 15 km W of Urbenville, NNSW (28°27'S, 152°24'E), 810 m (7, AMC154730, 18 May 1976, P.H. Colman, I. Loch); Red Scrub F.R., Whian Whian S.F., NNSW (28°38'S, 153°19'E) 210 m (2, AMC154731, 15 May 1976, P.H. Colman, I. Loch).

OTHER MATERIAL

Western end, Gibralter Range, NENSW (29°33'S, 152°17'E) NVF, under moss on rock (1, QMMO17272, 8 Mar 1987, J. Stanisic, D. Potter); top of Condamine River valley, along Croftby Rd (28°15'S, 152°29'E) (2, QMMO10541, Mar 1981, AM/QM-ABRS); Gibralter Range, NENSW, rainforest, litter (1, QMMO17275, 10 Nov 1980, R. Raven).

DIAGNOSIS

Shell minute, glossy, depressed, diameter 2.30–2.73 mm (mean 2.49 mm) with 3 3/4- to 4 1/4- (mean 4-) loosely coiled whorls. Last whorl (in adult specimens) descending much more rapidly. Apex and spire (Fig. 117c) strongly elevated, SP/BWW ratio 0.29–0.45 (mean 0.37), height 1.36–1.70 mm (mean 1.49 mm), H/D ratio 0.58–0.63 (mean 0.60). Protoconch of 1 5/8 to 1 3/4 whorls, mean diameter 629.7 μm at 1 1/2 whorls. Apical sculpture (Fig. 117f) of curved radial ribs, becoming more crowded toward the nuclear-postnuclear boundary, and low spiral cords. Postnuclear sculpture (Figs. 117e,h) consisting of widely spaced, prominent, protractively sinuated radial ribs which have large wing-like periostracal processes at the periphery; processes deciduous and not present in larger, worn specimens. Microsculpture (Fig. 117g) of numerous, fine, thread-like radials, crossed by low, crowded spiral cords. Sculpture continuous on the base. Umbilicus (Fig. 117b) narrow, U-shaped, diameter 0.41–0.82 mm (mean 0.60 mm), D/U ratio 3.32–5.60 (mean 4.38). Sutures impressed, whorls strongly shouldered above and rounded below a flattened periphery (Fig. 117c). Aperture roundly lunate. Lip simple, columella slightly dilated. Parietal callus strongly developed, connecting lip margins. Colour yellow-horn. Often covered in dirt particles. Based on 3 measured specimens.

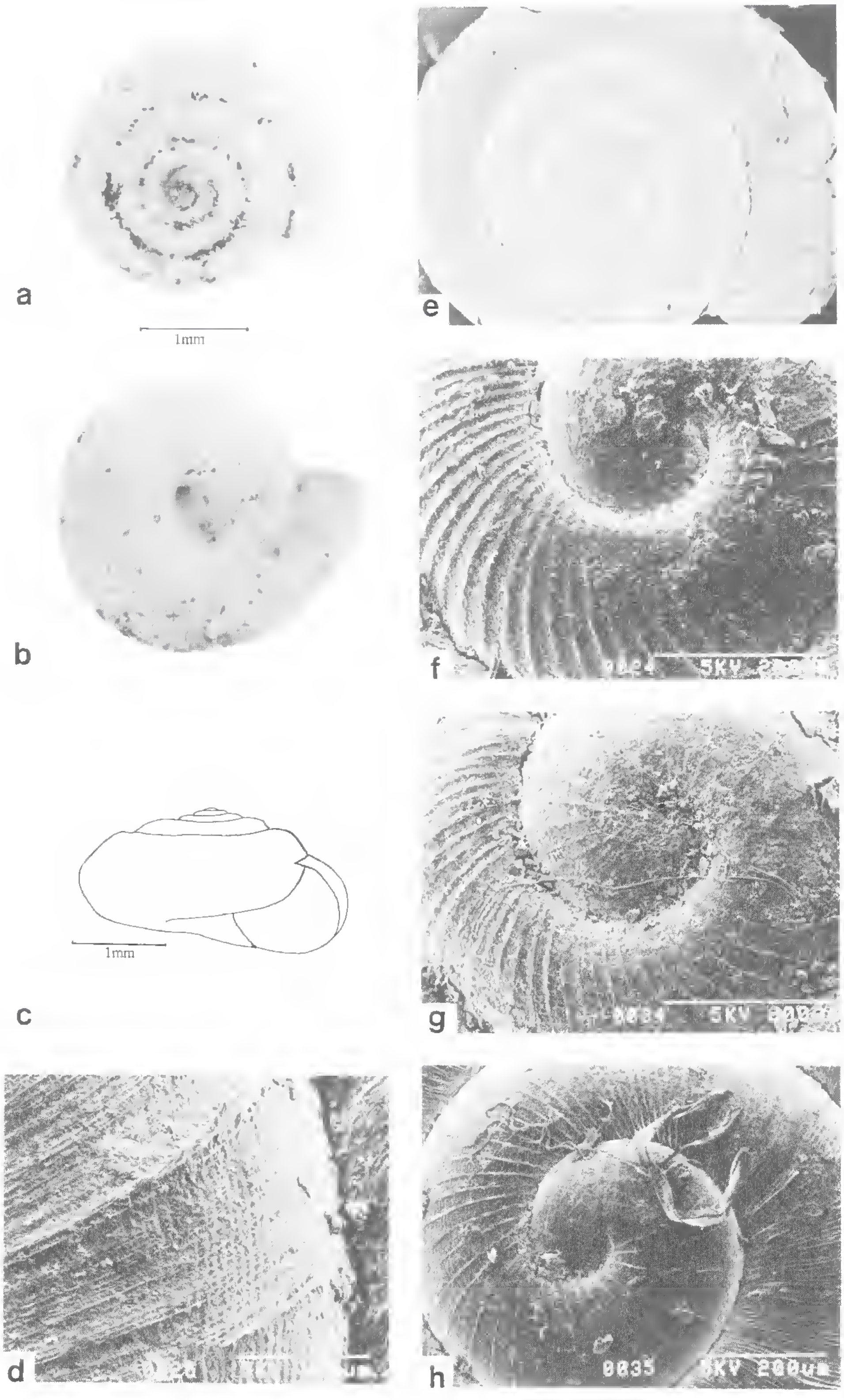
Genitalia with a short, expanded epiphallus bound to the penis sheath for its entire length (Fig. 118b). Epiphallus tubular, entering penis apically through a fleshy pilaster, internally with longitudinal thickenings. Penial retractor muscle inserted on epiphallus prior to the epiphallus-penis junction, usually originating from the diaphragm but in figured specimen (QMMO10691), arising from tentacular branch of columellar muscle. Penis (Fig. 118b) tubular, swollen apically, with a sheath in the expanded upper portion; internally with apical pustulations and basal spongy longitudinal pilasters.

Radula (Fig. 117d) typical.

Based on four dissected specimens (QMMO-

TABLE 24 - LOCAL VARIATION IN *COENOCHAROPA YESSABAHENSIS* SP. NOV., *COENOCHAROPA PARVICOSTATA* SP. NOV. AND *COENCOHAROPA MULTIRADIATA* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Coenocharopa yessabahensis												
Yessabah Caves QMMO 17261 (Holotype)	1	4 3/4	2.22	3.75	0.59	0.30	1.24	0.24	---	---	0.88	4.24
QMMO 17013	7	4 1/4+ (4 1/8–4 3/8+)	1.87±0.047 (1.70–2.04)	3.46±0.081 (3.24–3.83)	0.54±0.01 (0.48–0.56)	0.23±0.015 (0.17–0.30)	1.16±0.015 (1.11–1.24)	0.19±0.01 (0.15–0.26)	---	---	0.87±0.031 (0.78–1.03)	3.98±0.08 (3.73–4.30)
AMC 121680	12	4 3/8- (4 1/8-to4 5/8)	1.85±0.024 (1.66–1.96)	3.33±0.024 (3.19–3.45)	0.56±0.01 (0.50–0.61)	0.22±0.012 (0.13–0.26)	1.15±0.012 (1.11–1.24)	0.19±0.01 (0.11–0.23)	---	---	0.80±0.008 (0.76–0.82)	4.19±0.03 (4.05–4.43)
Coenocharopa parvicostata												
Mt Mee QMMO 17266 (Holotype)	1	4 3/8	1.58	2.81	0.56	0.30	0.94	0.32	---	---	0.84	3.34
Mt Mudlo QMMO 8358	5	4- (3 7/8-to4 1/8-)	1.41±0.031 (1.32–1.49)	2.48±0.016 (2.43–2.51)	0.57±0.01 (0.53–0.60)	0.18±0.016 (0.13–0.21)	0.84±0.022 (0.77–0.89)	0.21±0.02 (0.16–0.25)	---	---	0.60±0.015 (0.55–0.64)	4.15±0.12 (3.94–4.54)
QMMO 12355	2	3 7/8-	1.28±0.043 (1.24–1.32)	2.24±0.149 (2.09–2.39)	0.57±0.02 (0.55–0.59)	0.15±0.021 (0.13–0.17)	0.77±0.043 (0.72–0.81)	0.20±0.04 (0.16–0.23)	---	---	0.53±0.082 (0.45–0.67)	4.25±0.38 (3.87–4.62)
Kenilworth QMMO 17267	1	4 3/8+	1.49	2.47	0.60	0.170	0.937	0.18	---	---	0.55	4.46
Dandabah QMMO 6087	1	3 3/4	1.28	2.26	0.57	0.13	0.81	0.16	---	---	0.49	4.58
Tooloom QMMO 10936	3	4+ (3 7/8–4 1/8)	1.28±0.025 (1.24–1.32)	2.26±0.043 (2.17–2.30)	0.57	0.17±0.025 (0.13–0.21)	0.81	0.21±0.03 (0.16–0.26)	21	2.97	0.56±0.025 (0.51–0.60)	4.03±0.11 (3.87–4.23)
Mt. Pikapene QMMO 16946	1	3 7/8-	1.07	2.13	0.50	0.17	0.68	0.25	---	---	0.49	4.32
Diehappy S.F. QMMO 10824	2	4+ (4+to4 1/4+)	1.28	2.34±0.086 (2.26–2.43)	0.55±0.02 (0.53–0.57)	0.15±0.025 (0.13–0.17)	0.81	0.19±0.03 (0.16–0.21)	---	---	0.57±0.072 (0.51–0.64)	4.20±0.39 (3.81–4.58)
Dorrigo N.P. QMMO 10782	1	4 1/8-	1.32	2.17	0.61	0.17	0.77	0.22	---	---	0.51	4.23
Coenocharopa multiradiata												
Wilson's Peak QMMO 18973 (Holotype)	1	4 1/8	1.17	2.16	0.54	0.10	0.74	0.14	47	6.92	0.55	3.93
Carrai Caves AMC 142958	4	4- (3 7/8-to4 1/8+)	1.13±0.022 (1.09–1.19)	2.06±0.040 (1.95–2.14)	0.55±0.010 (0.53–0.57)	0.09±0.013 (0.06–0.12)	0.74±0.005 (0.72–0.74)	0.12±0.018 (0.08–0.16)	40.0±1.00 (40–42)	6.18±0.216 (5.78–6.52)	0.51±0.015 (0.47–0.53)	4.08±0.096 (3.94–4.36)
AMC 153728	1	3 7/8	1.17	2.11	0.55	0.10	0.74	0.14	---	---	0.53	3.98
Mt. Pikapene S.F. QMMO 10893	4	4- (3 7/8–4 1/8)	1.13±0.035 (1.07–1.19)	1.96±0.021 (1.91–2.01)	0.58±0.018 (0.54–0.62)	0.09±0.005 (0.08–0.10)	0.70±0.015 (0.66–0.72)	0.12±0.009 (0.11–0.15)	44	7.15±0.185 (6.96–7.33)	0.51±0.010 (0.49–0.53)	3.88±0.051 (3.79–4.02)


a
1mm
b
1mm
c
d
e
f
g
h
0035 5KV 200um

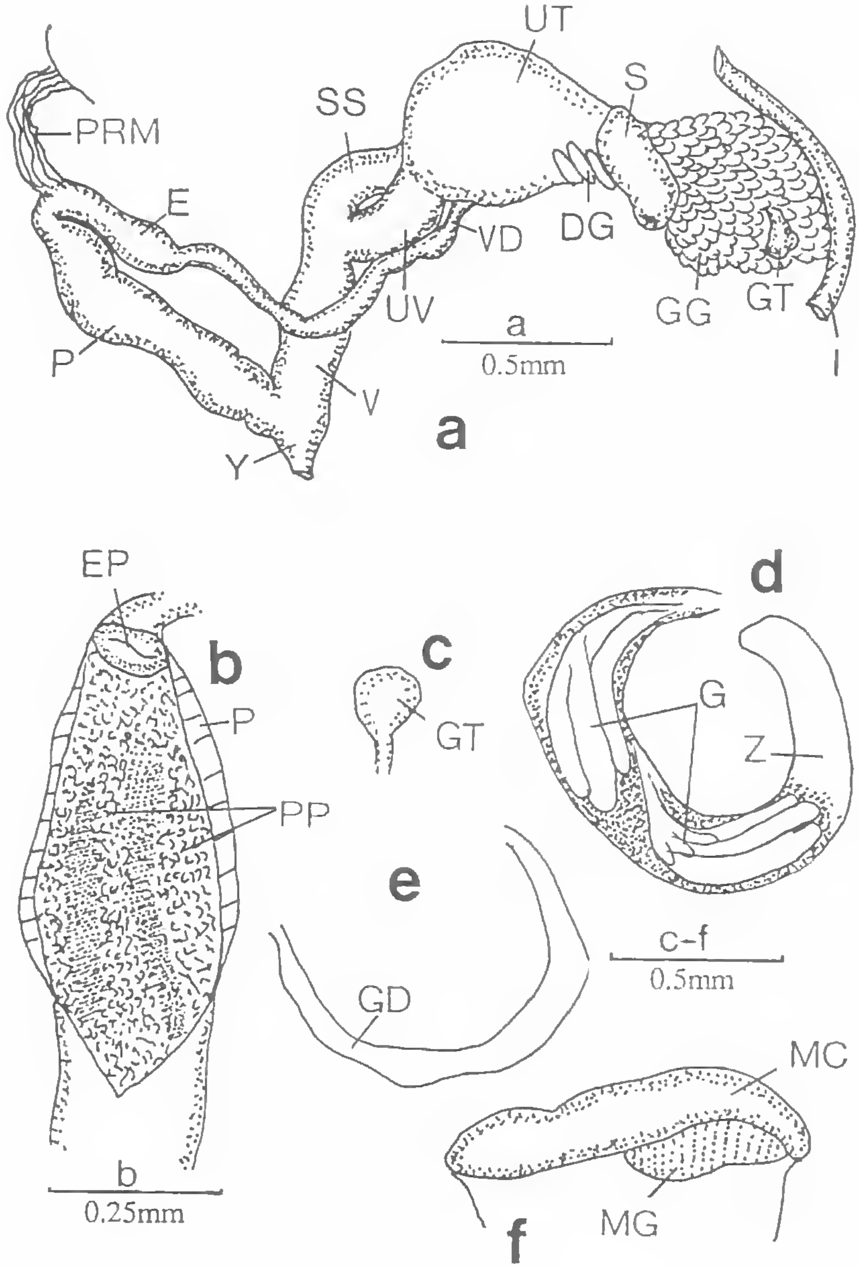


FIG. 121. *Coenocharopa parvicostata* sp. nov. Kenilworth S.F., SEQ. QMMO17264, paratype. a, genitalia; b, details of penis interior; c, talon; d, ovotestis; e, hermaphroditic duct; f, anterior edge of pallial cavity. Scale lines as marked.

FIG. 120. *Coenocharopa parvicostata* sp. nov. a–c, Freds Rd, Mt Mee, SEQ. QMMO17266, holotype; d–f, Mt Mudlo, Kilkivan S.F., SEQ. QMMO8358, paratype; g, Diehappy S.F., NSW. AMC128388, paratype; h, c. 8.3km from Woodenbong-Legume Rd, Tooloom Scrub, Beaury S.F., NSW. AMC128532, paratype. a–c, entire shell; d, post nuclear sculpture; e, spire; f–h, apical sculpture. Scale lines as marked.

10270, QMMO10269, QMMO17289, AMC-128563).

RANGE AND HABITAT

Cooler subtropical notophyll vine forests of the Great Dividing Range between Dorrigo, NSW and the QLD/NSW border, and the notophyll vine forests (and possibly microphyll fern forests) of the McPherson Ranges, SEQ. Live specimens have been collected from among moss on logs and rocks.

REMARKS

Probably '*Setomedea*' *aculeata* (Hedley 1899) comes closest in shell form. However, the periostracal extensions of '*S*'. *aculeata* are more slender, more numerous and regularly spaced along the major radial ribs.

Coenocharopa parvicostata sp. nov.
(Figs 120–122; Tables 22, 24)

ETYMOLOGY

Latin *parvus*, small; and *costatus* rib; refers to the postnuclear sculpture.

COMPARISONS

C. parvicostata is sympatric with *C. sordidus*, *C. macromphala* and *C. multiradiata*, and dead shells of these species are apt to be confused. However *C. parvicostata* can be distinguished from *C. sordidus* by its smaller size, more rounded whorls, less elevated spire and more prominently sculptured apex; from *C. macromphala* by the lack of a supraperipheral sulcus, less elevated spire and smaller umbilicus; from *C. multiradiata* by the more numerous apical radial ribs which are crowded at the nuclear-postnuclear boundary; and from *C. alata*, by having a less elevated spire and more rounded whorls.

TYPE MATERIAL

HOLOTYPE: QMMO17266, Fred's Road, Mt Mee, SEQ, 27°05'S, 152°43'E, rainforest, litter. Collected by J. Stanisic, N. Hall, A. Green, 14 Apr 1980. Height of shell 1.58 mm, diameter 2.81 mm, H/D ratio 0.56, D/U ratio 3.34, whorls 4 3/8.

PARATYPES: Mt Mudlo, Kilkivan S.F., SEQ (26°01'S, 152°13'E), NVF/*Araucaria*, leaf litter (9, QMMO8358, 17 Jul 1980, J. Stanisic, A. Green); Kenilworth S.F., SEQ (26°37'S, 152°42'E) rainforest, leaf litter (1, QMMO17267, 22 May 1980, J. Stanisic, A. Green); c. 8.3 km from Woodenbong - Legume Road, Tooloom Scrub, Beaury S.F., NENSW (28°29'S, 152°24'E) CNVF (7, AMC128532, QMMO10936, 15 Mar 1981, AM/QM-ABRS); Dandabah, Bunya Mts N.P., SEQ (26°53'S, 151°35'E) (2, QMMO6087, 5 Mar 1976, M.J. Bishop); c. 6.5 km E of tickgate, Mt Pikapene S.F., NENSW, (29°01'S, 152°45'E) rainforest (1, QMMO16946, Mar 1981, AM/QM-ABRS); creek cutting, Diehappy S.F., NENSW (30°28'S, 152°38'E), broad leaf scrub (7, QMMO10824, AMC128388, Mar 1981 AM/QM-ABRS); Newell Falls, Dorrigo N.P., NENSW (30°24'S, 152°45'E) NVF (6, QMMO10782, AMC-128333, Mar 1981, AM/QM-ABRS); Mudlo Gap S.F., SEQ (26°01'S, 152°14'E) MVF/*Araucaria* (5, QMMO12355, AMC136656, 2 Sept 1982, AM/QM-ABRS); c. 0.5 km S of 'Bellbird' parking area, Kenilworth S.F., SEQ, rainforest litter (1, QMMO17264, 28 Feb 1980, J. Stanisic, A. Green).

OTHER MATERIAL

Little Yabba Creek, Imbil S.F., SEQ (26°28'S, 152°38'E) NVF (5, QMMO12026, AMC136440, 8 Sept 1982, AM/QM-ABRS); Bellinger River, NENSW (30°27'S, 152°37'E) rainforest gully (3, QMMO10832, AMC128399, Mar 1981, AM/QM-ABRS); Mt Warning N.P., NENSW, near base (28°24'S, 153°16'E) NVF/Palms (4, QMMO10480, AMC129285, Mar 1981, AM/QM-ABRS); side track off Mt Archer Rd, Mt Mee S.F., SEQ (27°04'S, 152°41'E), NVF/*Araucaria* (1, QMMO15079, J. Stanisic, D. Potter); Manorina N.P., Mt Nebo, SEQ (27°23'S, 152°47'E) wet sclerophyll (1, QMMO6258, Aug 1976, M.J. Bishop); Wratten's Camp, Wrattens S.F., SEQ (26°17'S, 152°20'E) NVF, litter (3, QM-MO11563, 17 Jul 1980, J. Stanisic, A. Green); Cherry Tree North S.F., c. 40 km W of Casino, NSW (28°54'S, 152°45'E), 400 m (100 +, AMC154733, 19 May 1976, P.H. Colman, I. Loch); Red Scrub F.R., NENSW (28°38'S, 153°20'E), rainforest (1, AMC128867, 20 Mar 1981, AM/QM-ABRS); Mt Lindesay, Upper Richmond Rv, NSW (3, AMC154734, 27 Apr 1948, L. Price); Koreelah Ck, Beaury S.F., c. 15 km W of Urbenville, NSW (28°31'S, 152°20'E) (52, AMC154736, 18 May 1976, P.H. Colman, I. Loch).

DIAGNOSIS

Shell small, depressed, diameter 2.09–2.81 mm (mean 2.36 mm) with 3 3/4 to 4 1/4 (mean 4+) whorls, last whorl descending. Spire (Fig. 120c) moderately elevated to depressed, SP/BWW ratio 0.16–0.32 (mean 0.21). Height 1.07–1.58 mm (mean 1.24 mm), H/D ratio 0.50–0.61 (mean 0.57). Protoconch of 1 1/4 to 1 5/8 whorls, mean diameter 564.5 μm at 1 1/2 whorls. Apical sculpture (Fig. 120f–h) of fine, protrac-

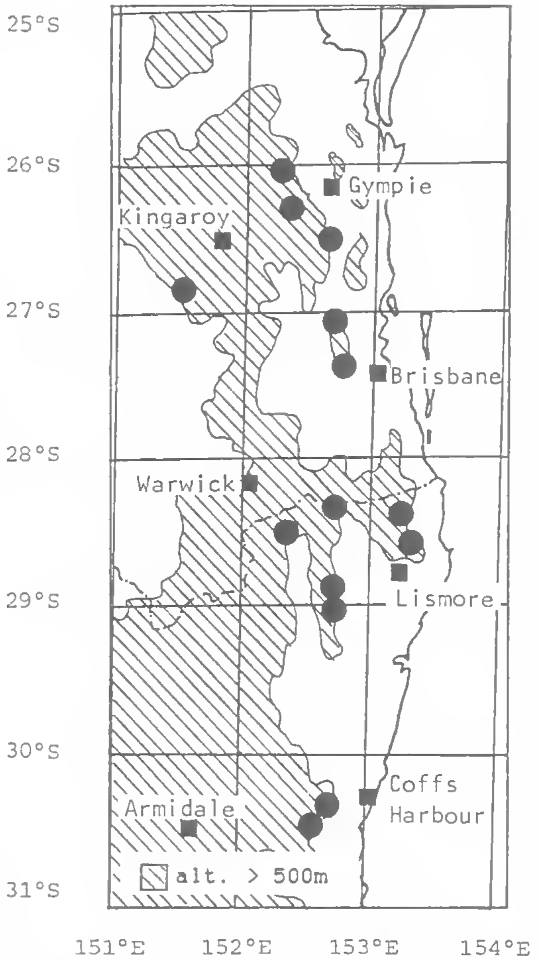


FIG. 122. Distribution of *Coenocharopa parvicostata* sp. nov.

tively sinuated radial ribs, more crowded near the nuclear-postnuclear boundary, crossed by irregular spiral cords. Postnuclear sculpture (Fig. 120d) of regularly spaced (often obsolete) blade-like, protractively sinuated radial ribs, continuous on the base. Microsculpture (Fig. 120d) of numerous, thread-like radial riblets and low, broad crowded spiral cords. Umbilicus wide, V-shaped, diameter 0.45–0.84 mm (mean 0.57 mm). D/U ratio 3.34–4.62 (mean 4.16). Sutures impressed; whorls rounded below and slightly shouldered above the periphery (Fig. 120c). Aperture roundly to ovately lunate. Lip simple, columella dilated and twisted toward the umbilicus. Parietal callus present. Colour light-yellow horn with a pink tinge in some specimens.

Genitalia with epiphallus (Fig. 121a) tubular, internally with longitudinaly thickenings, entering the penis apically through a simple pore surrounded by a muscular collar (Fig. 121b). Penial retractor muscle inserting on the epiphallus prior to its entry into the penis chamber. Penis (Fig. 121b) expanded, tubular, internally with crowded pustulations and weak longitudinal pilasters. Vagina short, expanded, internally with spongy pustulations.

No data available on radula.

Based on one dissected specimen (QMMO-17264).

Range and Habitat

From the Dorrigo area, northern NSW to Mt Mudlo, north of Gympie, SEQ. It has the largest distribution of any *Coenocharopa* species and is found in both warm moist notophyll vine forest and drier araucarian notophyll vine forest. Although there is some range overlap with *C. alata*, *C. parvicostata* has only been found sympatrically with that species in the Beaury State Forest, northern NSW. No data available on microhabitat.

Remarks

In spite of the comparatively large number of dead shells available for study only one subadult specimen was suitable for dissection and more material is needed to confirm structures of the terminal male genitalia. As may be expected in a wide ranging species there is a degree of interpopulational variation in shell characters. Southern specimens are larger and have bolder sculpture on the protoconch.

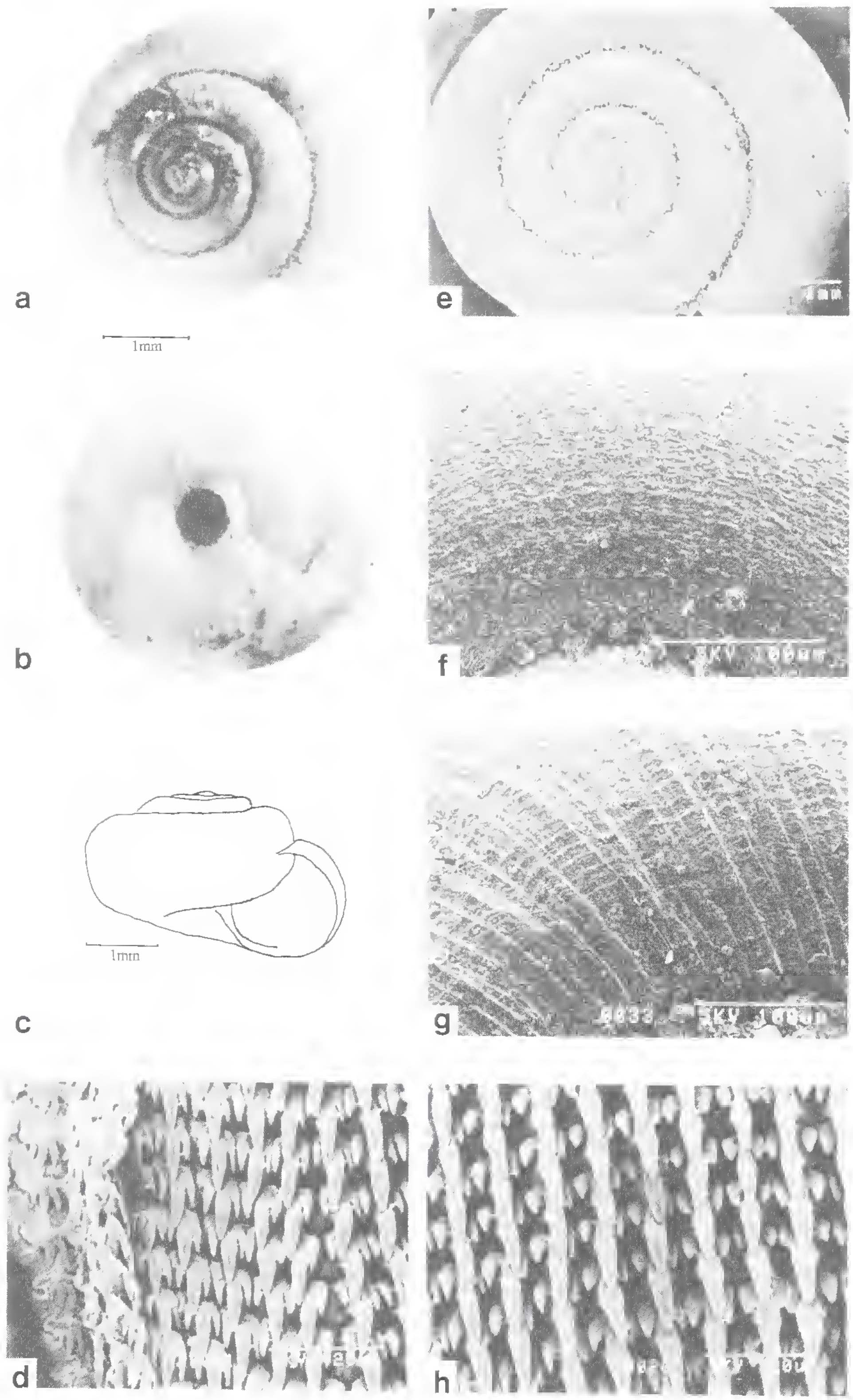
Coenocharopa yessabahensis sp. nov.
(Figs 123–125; Tables 22, 24)

Etymology

For the type locality, Yessabah.

Comparisons

Its relatively large size and postnuclear sculpture of numerous low, crowded, radial ribs distinguish *C. yessabahensis* from congeners. *C. sordidus* is most similar but has widely spaced radial ribs with conspicuous periostracal blades. Anatomically the penial pilaster pattern of apical stimulatory pad and large basal U-shaped thickening contrasts with the typical pattern of simple longitudinal thickenings. *C. multiradiata* which is possibly sympatric with *C. yessabahensis*, has regular widely spaced radial ribs, more conspicuous microsculpture and is much smaller.


a
1mm
b
c
1mm
d
e
f
g
h

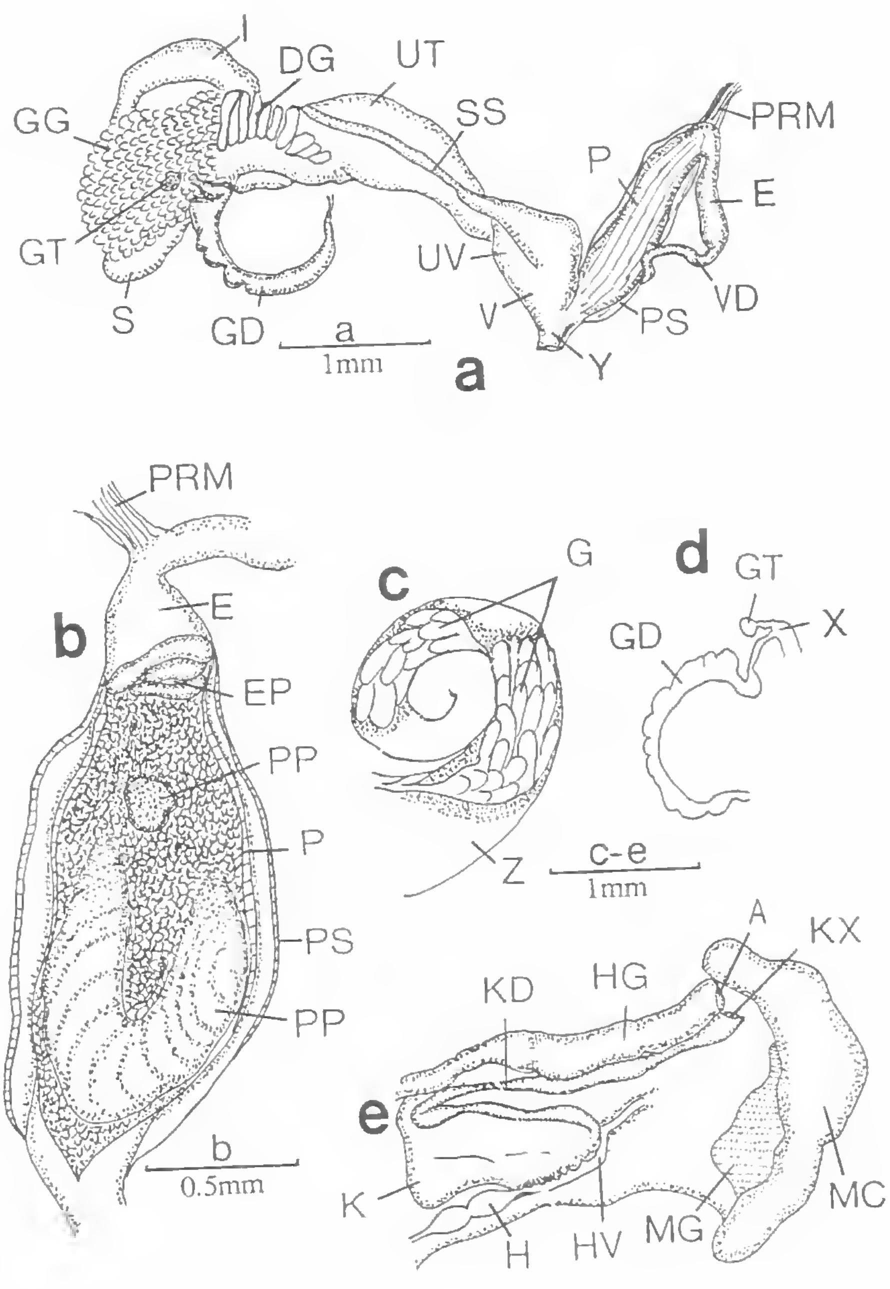


FIG. 124. *Coenocharopa yessabahensis* sp. nov. Yessabah Caves, via Kempsey, NSW. QMMO17013, paratype. a, genitalia; b, details of penis interior; c, ovotestis; d, hermaphroditic duct and talon; e, pallial cavity. Scale lines as marked.

FIG. 123. *Coenocharopa yessabahensis* sp. nov., a–c, Yessabah Caves, via Kempsey, NSW. QMMO17261, holotype; d–h, same data as holotype. QMMO17013, AMC121680, paratypes. a–c, entire shell; d, marginal teeth; e, spire; f, apical sculpture; g, post nuclear sculpture; h, central and lateral teeth. Scale lines as marked.

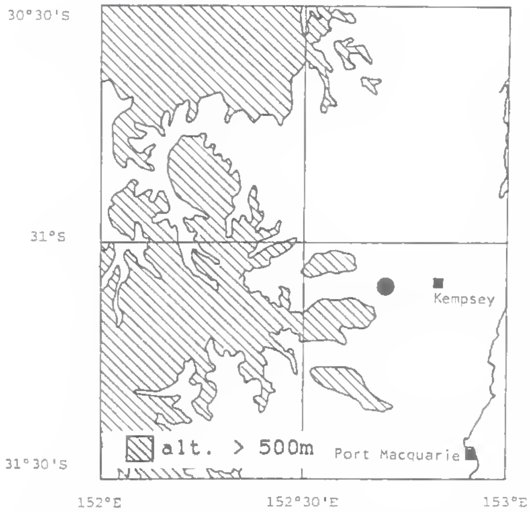


FIG. 125. Distribution of *Coenocharopa yessabahensis* sp. nov.

TYPE MATERIAL

HOLOTYPE: QMMO17261, Yessabah Caves, via Kempsey, NENSW (31°05'30"S, 152°51'E), vine thicket on limestone rocks. Collected by J. Stanisic, D. Potter, P.H. Colman, 3 March 1987. Height of shell 2.22 mm, diameter 3.75 mm, H/D ratio 0.59, D/U ratio 4.24, whorls 4 3/4.

PARATYPES: 130 live, and 20 dead adults and subadults, QMMO17013, same data as holotype; Yessabah limestone cave, Sherwood Quarry, W of Kempsey, NSW (31°06'S, 152°42'E), ground litter in and out of cave (63, AMC121680, 9 Oct 1979, P.H. Colman, J. Stanisic).

DIAGNOSIS

Shell small, depressed, diameter 3.19–3.83 mm (mean 3.40 mm), with 4 1/8 to 4 3/4 (mean 4 3/8) normally coiled whorls. Last whorl descending slightly in front. Apex and spire (Fig. 123c) only slightly elevated, SP/BWW ratio 0.11–0.26 (mean 0.20). Height 1.66–2.22 mm (mean 1.88 mm). H/D ratio 0.48–0.61 (mean 0.55). Protoconch shiny with 1 1/4 to 1 5/8 whorls, mean diameter 644.5 μm at 1 1/2 whorls. Apical sculpture (Fig. 123f) of weak, squiggly, irregularly spaced spiral cords and vague, low radial ribs. Postnuclear sculpture (Fig. 123g) of low, broad, crowded spiral cords, crossed by weak thread-like radial and microradial ribs, continuous on the base. Umbilicus (Fig. 123b) narrow, U-shaped, diameter 0.76–1.03 mm (mean 0.83 mm). D/U ratio 3.73–4.43 (mean 4.12). Sutures strongly impressed; whorls shouldered above and rounded below the periphery (Fig. 123c). Aperture roundly lunate. Lip simple, slightly thickened at the columellar margin. Columella dilated and slightly reflected over the umbilical opening. Parietal callus developed. Colour yellowy-brown. Based on 20 measured adults.

Body colour dark grey, with ommatophores and pedal glands darker. Terminal male genitalia with epiphallus (Fig. 124a) reflexed, entering the penis apically through two spongy thickenings. Penis (Fig. 124b) thick, muscular with a thin sheath for its entire length; internally with a spongy horseshoe-shaped pilaster (Fig. 124b) in lower part of the penial chamber, and a small subcircular thickening in the apical half, otherwise with pustules. Penial retractor muscle inserted on the epiphallus prior to its junction with the penis. Free oviduct short, muscular, internally with rather vague, transverse, spongy thickenings. Vagina short, thin with internal longitudinal pilasters.

Radula (Fig. 123d,h) with mesocone of the central and inner laterals greatly enlarged.

Based on four dissected adults (QMMO-17013).

RANGE AND HABITAT

Only on the limestone outcrop at Yessabah, near Kempsey, NSW, which supports a low vine thicket. Crawling on limestone rocks.

REMARKS

C. yessabahensis, *Letomola contortus* and *Rhophodon kempseyensis* are restricted to the limestone outcrops between Yessabah and Carrai, near Kempsey, NSW suggesting that these outcrops are important refugia for terrestrial snails.

Coenocharopa multiradiata sp. nov.
(Figs 126–127; Tables 22, 24)

ETYMOLOGY

Latin *multi* -, many; and *radiata* radial; referring to the numerous radial ribs.

COMPARISONS

Sculpturally, *C. multiradiata* is the most distinctive species of *Coenocharopa* described herein. The sculpture is regular and in many ways simulates the more typical reticulate pattern seen in *Gyrocochlea* and *Rhophodon*. Compared with its congeners, *C. multiradiata* has

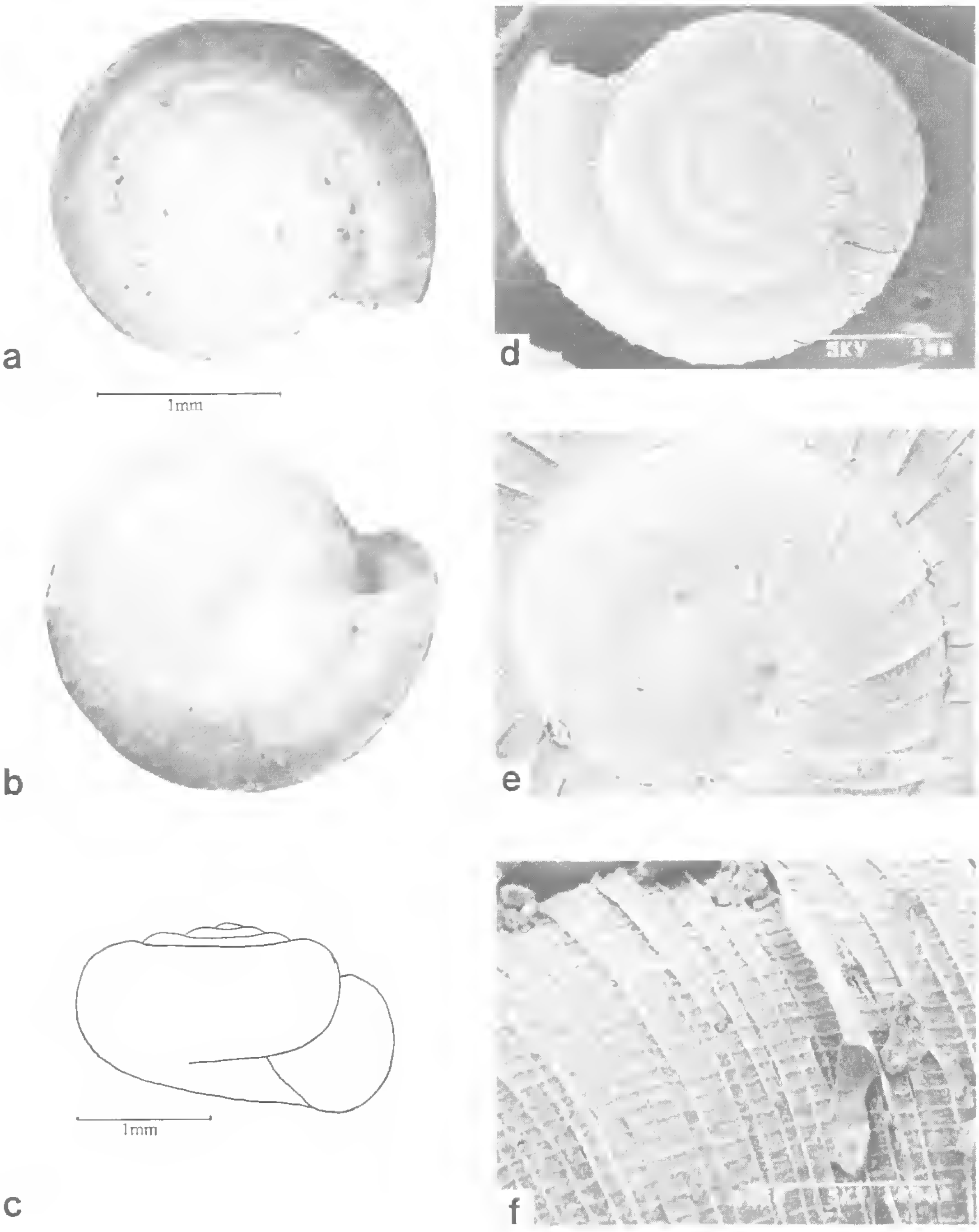


FIG. 126. *Coenocharopa multiradiata* sp. nov. a-c, Top of Condamine River valley on W slopes of Wilson's Peak along Croftby Rd, NSW. QMMO18973, holotype; d-f, Natural Arch, Carrai Caves, NSW, AMC 142958, paratype. a-d, entire shell; e, apical sculpture; f, post nuclear sculpture. Scale lines as marked.

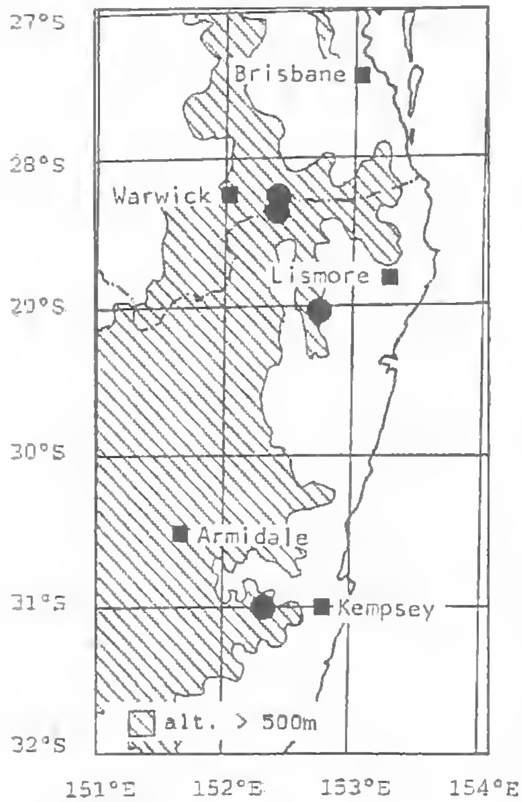


FIG. 127. Distribution of *Coenocharopa multiradiata* sp. nov.

more numerous, less protractively sinuated radial ribs and microradials which have conspicuous periostracal blades. In addition, the microspirals are less crowded, more slender and raised to produce a conspicuous reticulate pattern. *C. alata* is larger, has fewer radial ribs with extremely expanded periostracal processes and has a more reduced microsculpture. *C. parvicostata* which is most apt to be confused with *C. multiradiata*, is larger with more elevated spire and has fewer, less regularly spaced, more protractively sinuated radial ribs. In subadult specimens, these two species can be differentiated by their apical sculpture which consists of few, widely spaced, well defined, radial ribs in *C. multiradiata*, and crowded, low ridges, becoming more crowded at the nuclear-postnuclear boundary, in *C. parvicostata*. *C. yessabahensis* is larger with very crowded, weak, radial ribs and reduced microsculpture.

TYPE MATERIAL

HOLOTYPE: QMMO18973, top of Condamine River valley on W slopes of Wilson's Peak, along Crofthy Road, SEQ (28°16'S, 152°28'E), rainforest/hoop pine. Collected AM/QM-ABRS, 16 Mar 1981. Height of shell 1.17 mm, diameter 2.16 mm, H/D ratio 0.54, D/U ratio 3.93, whorls 4 1/8.

PARATYPES: AMC128634, same collection data as holotype; Natural Arch, Carrai Caves, near Kempsey, NSW, leaf litter (9, AMC142958, 22 Feb 1980, P.H. Colman); c. 6.5 km E of Tickgate, Mt Pikapene S.F., NSW (28°01'S, 152°45'E), riverine rainforest (11, QMMO10893, 14 Mar 1981, AM/QM-ABRS).

OTHER MATERIAL

Limestone caves at Natural Arch, W of Kempsey, NSW (30°59'S, 152°21'E), under slabs of limestone (7, AMC143728, 10 Mar 1981, W. Ponder, O. Griffiths); Koreelah S.F., NSW, c. 12.2 km from Acacia Plateau-Killarney Rd, (28°21'S, 152°24'E) SEVT/MVF (1, AMC128553, 15 Mar 1981, AM/QM-ABRS).

DIAGNOSIS

Shell diameter 1.91–2.16 mm (mean 2.03 mm), with 3 7/8- to 4 1/8+ (mean 4-) normally coiled whorls, last whorl descending slightly. Apex and spire (Fig. 126c), very slightly elevated, SP/BWW ratio 0.08–0.16 (mean 0.13), height of shell 1.07–1.19 mm (mean 1.14 mm), H/D ratio 0.43–0.62 (mean 0.54). Protoconch of 1 1/2 to 1 5/8 whorls, mean diameter 511.1 μm at 1 1/2 whorls. Apical sculpture (Fig. 126e) consisting of widely spaced, conspicuous, slightly curved radial ribs with raised periostracal blades and numerous, narrow, low spiral cords. Post nuclear sculpture (Fig. 126f) of numerous, regularly spaced, weakly protractively sinuated radial ribs which have prominent periostracal blades that are often worn, 38–47 (mean 42.5) ribs on the body whorl. Ribs/mm 5.78–6.96 (mean 6.63). Microsculpture (Fig. 126f) of fine thread-like radial riblets, 6–13 between each pair of major ribs, and fine, slender conspicuous spiral cords which are not raised at their junction with the microradials. Sculpture continuous on the base. Umbilicus (Fig. 126b) narrow, U-shaped, diameter 0.47–0.55 mm (mean 0.51 mm). D/U ratio 3.79–4.36 (mean 3.98). Sutures impressed, whorls shouldered above and rounded below a slightly flattened periphery (Fig. 126c). Aperture roundly lunate. Lip simple, columella not expanded. Parietal callus developed. Colour light-horn. Based on 10 measured adults.

Anatomy unknown.

RANGE AND HABITAT

From the top of the Richmond Range, NSW and from the Carrai limestone outcrop near Kempsey, NSW; in dry cool subtropical vine forest and warm temperate rainforest. It is probable that *C. multiradiata* extends further south in warm temperate forest. No data are available on microhabitat.

REMARKS

C. multiradiata differs from average *Coenocharopa* patterns in a number of features. Nonetheless these altered character states are readily derived from typical *Coenocharopa*. In the absence of anatomical detail, placement in this genus is preferable to creating another nomenclatural entity based on shell characters.

Egilomen Iredale, 1937

Egilomen Iredale, 1937a, p. 328; Iredale, 1941a, pp. 267, 269; Kershaw, 1955, p. 29; Burch, 1976, p. 132.

TYPE SPECIES

Helix cochlidium Cox 1868; by original designation.

PREVIOUS STUDIES

Egilomen was introduced for five species with bold radial ribs and wide umbilicus. *Egilomen* is herein redefined to include species that have apical sculpture of prominent radial ribs with spiral elements absent or reduced, postnuclear sculpture of bold radial ribs, and a microsculpture of low rounded spiral cords. '*Helix*' *cochlidium*, and a new species from northern NSW and SEQ are assigned. Other species previously allocated to *Egilomen* probably belong elsewhere.

DIAGNOSIS

Shell diameter 1.62–3.07 mm, with 4 1/4 to 5 1/8 tightly coiled whorls, last descending rapidly. Apex and spire weakly to strongly (*globosa*) elevated. Apical sculpture of broad, bold, widely spaced, weakly curved radial ribs, and weak spiral cords. Postnuclear sculpture of broad, bold, moderately to widely spaced (*cochlidium*), weakly protractively sinuated to vertical radial ribs. Microsculpture of low, rounded, crowded spiral cords crossed by fine, thread-like radial riblets. Umbilicus wide, U-shaped (*cochlidium*) to closed (*globosa*). Sutures strongly impressed. Whorls shouldered above and rounded below a weakly compressed periphery. Lip thickened, rarely with a distinct basal knob (some populations of *globosa*), retracted at the suture to form an apertural sinus.

Animal with foot short and broad; colour white without any accessory pigmentation. Pallial cavity with complete secondary ureter and strongly bilobed kidney. Talon with very short stalk, subcircular. Terminal male genitalia with well-differentiated epiphallus and simple epiphallic pore. Penial retractor muscle inserting on epiphallus. Penis subcylindrical, internally with a single, large longitudinal pilaster and an accessory circular pad. Female genitalia with relatively long vagina and free oviduct. Radula with central tooth much smaller than laterals, otherwise without unusual features.

COMPARISONS

Conchologically *Egilomen* resembles *Cralopa* and *Rhophodon*. *Rhophodon* differs most markedly in having apertural barriers. Microsculpturally *Egilomen* (Figs 128g, 131f) has prominent, rounded, continuous spiral cords crossed by fine, thread-like radials in contrast to *Rhophodon*, which has low, barely visible spiral cords and prominent, high microradial ribs with elongate beads at their intersection (Figs 81f, 87e). Anatomically the strongly bilobed kidney of *Egilomen* (Figs 129d, 132f) contrasts with the weakly bilobed, to almost unilobed, condition of *Rhophodon* (Figs 72f, 75h). Terminal male genitalia of *Egilomen* have the penial retractor muscle inserted on the epiphallus (Figs 129b, 132b) whereas in *Rhophodon* it is always inserted at the penis-epiphallus junction (Figs 72a, 75e).

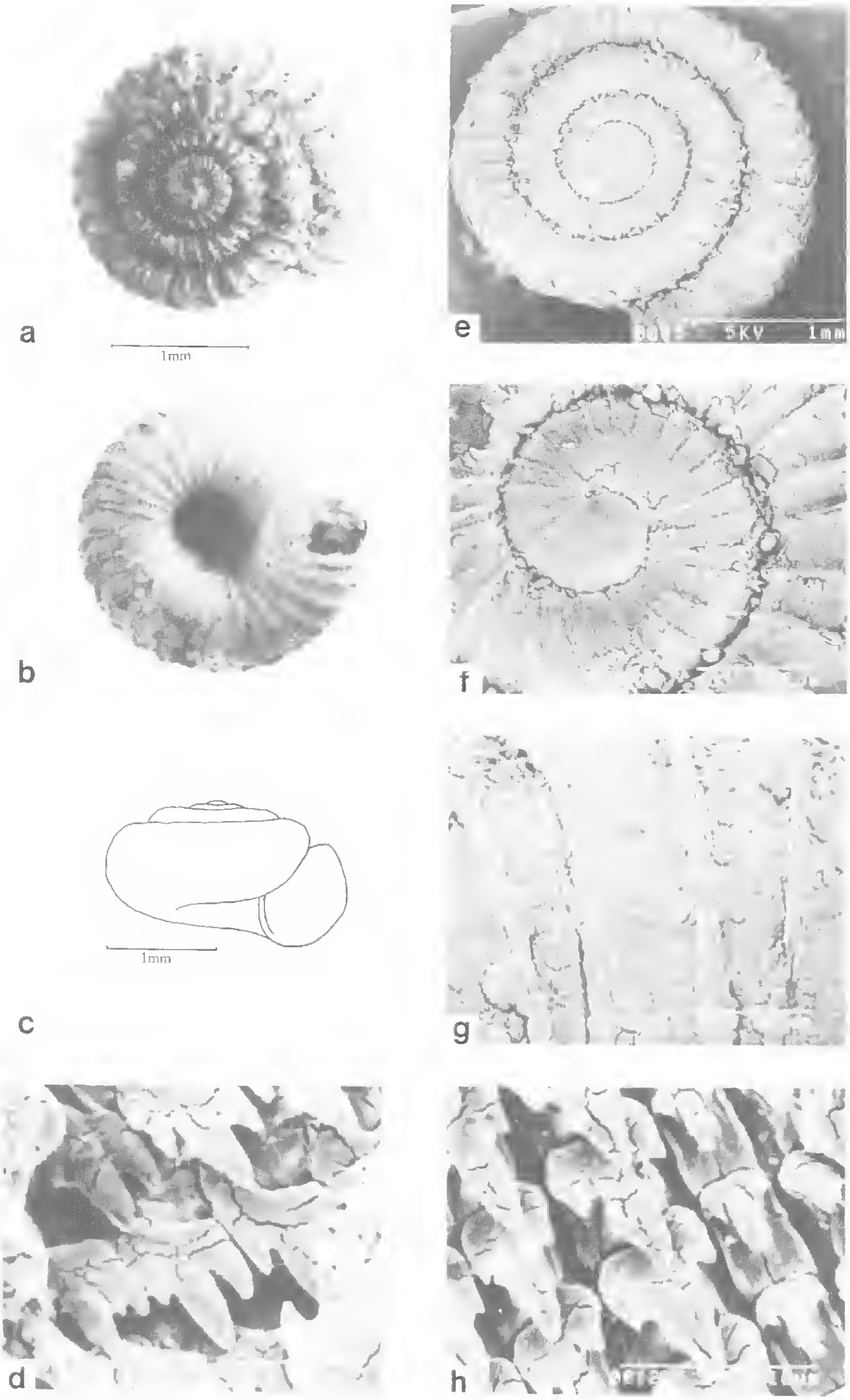
Cralopa differs in having more prominent apical spiral cords, more raised microsculpture and less differentiated epiphallus.

Egilomen cochlidium (Cox, 1868)
(Figs 128–130; Tables 22, 25)

Helix cochlidium Cox, 1868, p. 13, pl. 8, fig. 1.
Egilomen cochlidium (Cox); Iredale, 1937a, p. 328; Iredale, 1941a, p. 269.

COMPARISONS

E. cochlidium differs from *E. globosa* in its flattened shell and wide umbilicus. It is most similar to species of *Rhophodon* but lacks apertural barriers and has less crowded apical sculpture. *Discocharopa aperta* (Fig. 93) has a wide umbilicus and prominent radial sculpture but is


a
1mm
b
c
1mm
d
e
5KV 1mm
f
g
h

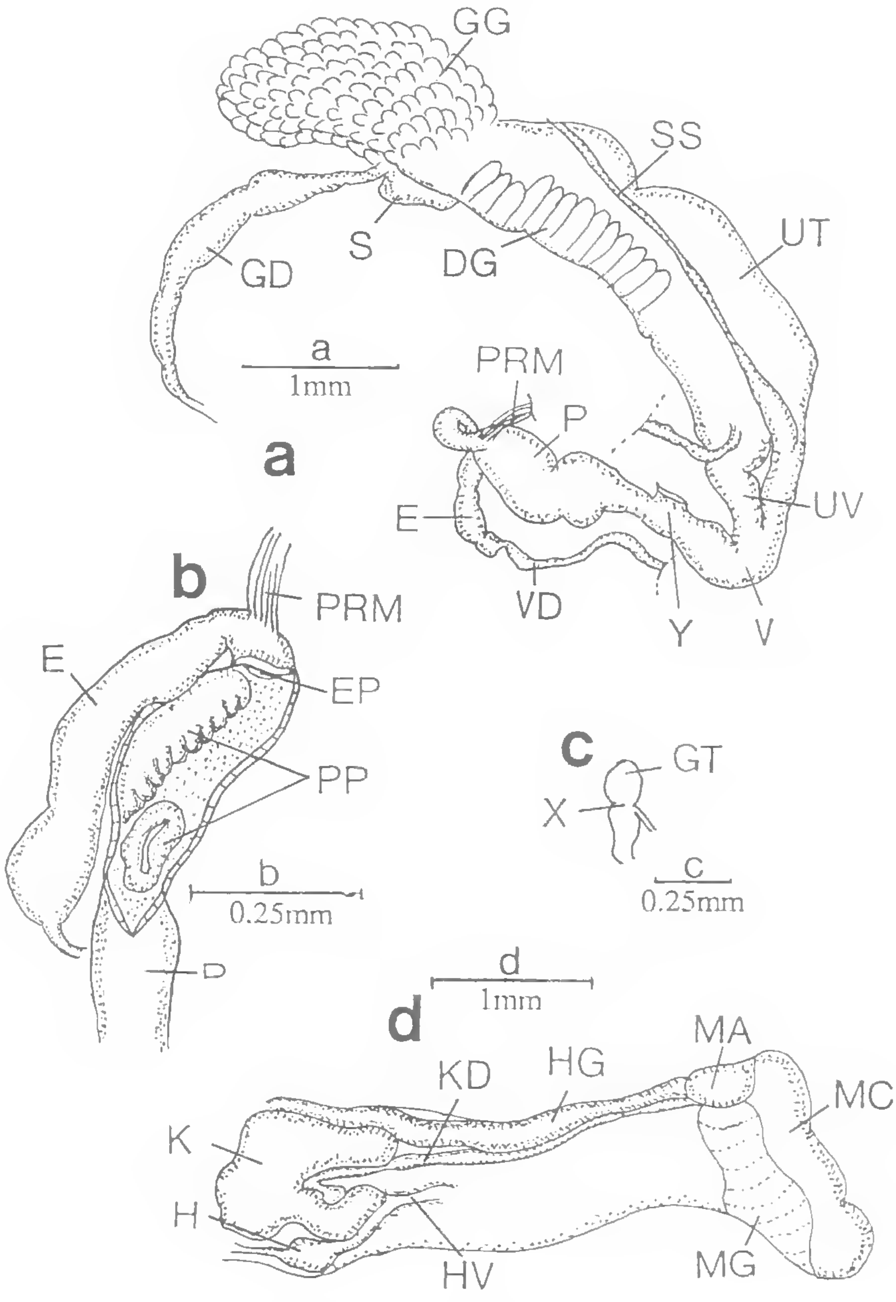


FIG. 129. *Egilomen cochlidium* (Cox, 1868). a, c, d, Upper Pine Ck, Canungra, SEQ. QMMO16905. b, Mills Rd, Moonpar S.F., NSW. QMMO17290. a, genitalia; b, details of penis interior; c, talon and carrefour; d, pallial cavity. Scale lines as marked.

FIG. 128. *Egilomen cochlidium* (Cox, 1868). a–c, Clarence River, NSW. AMC63505, lectotype; d, h, Mills Rd, Moonpar S.F., NSW. QMMO17290; e–g, The Island, off Grafton, NSW. AMC57247. a–c, entire shell; d, marginal teeth; e, entire shell; f, apical sculpture; g, post nuclear sculpture; h, central and lateral teeth. Scale lines as marked.

TABLE 25 - LOCAL VARIATION IN *EGILOMEN COCHLIDIUM* (COX, 1868) AND *EGILOMEN GLOBOSA* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Egilomen cochlidium												
Clarence River AMC 63505 (Lectotype)	1	4 1/2	1.25	2.26	0.55	0.10	0.76	0.14	30	4.22	0.72	3.14
AMC 153714	1	4 5/8	1.19	2.14	0.56	0.19	0.70	0.27	30	4.47	0.68	3.15
AMC 8737	1	4 1/4	1.17	2.01	0.58	0.16	0.64	0.23	33	5.22	0.72	2.80
Grafton AMC 57247	10	4 1/2+ (4-to4 7/8+)	1.33±0.074 (0.95–1.58)	2.39±0.110 (1.91–2.77)	0.55±0.011 (0.49–0.61)	0.22±0.078 (0.06–0.23)	0.80±0.038 (0.58–0.94)	0.18±0.016 (0.09–0.25)	39.1±1.47 (32–47)	5.33±0.143 (4.71–5.99)	0.86±0.036 (0.72–1.03)	2.77±0.526 (2.59–3.06)
Cherry Tree North S.F. AMC 153715	1	5 1/8-	1.83	3.07	0.60	0.27	0.98	0.27	45	4.67	0.88	3.47
Goomburra S.F. AMC 128618	1	4-	1.11	2.05	0.54	0.12	0.62	0.20	35	5.42	0.60	3.45
Egilomen globosa												
Mt Mee QMMO 17292 (Holotype)	1	4 3/4	1.57	2.47	0.76	0.43	0.80	0.48	67	8.63	—	—
QMMO 12178	6	4 1/2+ (4 3/8–4 5/8)	1.68±0.060 (1.49–2.04)	2.21±0.044 (2.00–2.34)	0.76±0.029 (0.71–0.96)	0.35±0.018 (0.26–0.43)	0.81±0.018 (0.72–0.89)	0.43±0.028 (0.30–0.53)	54.7±1.20 (53–57)	7.90±0.066 (7.75–8.08)	—	—
Mt Guyra QMMO 12068	4	4 3/4- (4 3/8–5+)	1.46±0.120 (1.19–1.66)	1.87±0.109 (1.62–2.09)	0.79±0.023 (0.74–0.83)	0.31±0.059 (0.17–0.43)	0.72±0.033 (0.64–0.77)	0.43±0.066 (0.25–0.55)	80	12.19	—	—
Mt Warning QMMO 10483	1	4 7/8	1.79	2.34	0.76	0.30	0.94	0.32	62	6.42	—	—

much smaller, lacks regular spiral sculpture and has finer, more crowded radial ribs.

TYPE MATERIAL

LECTOTYPE: AMC63505, Clarence River, NSW. Height of shell 1.25 mm, diameter 2.26 mm, H/D ratio 0.55. D/U ratio 3.14, whorls 4 1/2.

PARALECTOTYPES: AMC153714, 2 specimens, same collection data as holotype.

OTHER MATERIAL

Dorrigo, NSW (1, AMC63790); The Island, off Grafton, NSW (12, AMC57247); O'Reillys, Lamington N.P., SEQ (28°14'S, 153°15'E), MFF (1, AMC129243, 17 Mar 1981, AM/QM - ABRS); W side Richmond Range, NSW, tributary of Duck Ck (28°33'S, 152°40'E) (2, AMC128524, 14.Mar 1981, AM/QM - ABRS); top of Condamine River Valley, W slope of Wilson's Peak, NSW (28°16'S, 152°28'E) (1, AMC128637, 16 Mar 1981, AM/QM - ABRS); Upper Pine Creek, Canungra, SEQ, NVF/*Araucaria*, under rock (1, QMMO16905, 21 Jan 1987, J. Stanisic, D. Potter); Mills Rd. Moonpar S.F., NSW (30°13'S, 152°39'E) rainforest (1, QMMO17290, 7 Mar 1987, J. Stanisic, D. Potter); Carr's Creek, Clarence River, NSW (1, AMC8737, presented C. Hedley, ex Brazier, Rossiter. Cox: 1, AMC152253, ex Brazier); Cherry Tree North S.F., NSW (28°54'S, 152°45'E) litter (5, AMC153714, AMC154732. 19 May 1976, P.H. Colman, I. Loch); Goomburra S.F., SEQ (27°59'S, 152°21'E) (1, AMC128618, 16 Mar 1981 AM/QM - ABRS); N of Dorrigo, Clouds Ck S.F., NSW (30°07'S. 152°41'E) dense rainforest (1, AMC-128319, 11 Mar 1981, AM/QM - ABRS); c. 5.5 km N of Dorrigo NSW (30°23'S, 152°44'E) (1, QMMO-10794, Mar 1981, AM/QM - ABRS); Cunninghams Gap, SEQ, leaf litter (1, QMMO17291, 18 Jun 1979, G. Annabell); Koreelah Ck, Beaury S.F., NSW (28°-21'S, 152°20'E) (3, AMC154735, 18 May 1976, P.H. Colman, I. Loch).

DIAGNOSIS

Shell diameter 1.91–3.07 mm (mean 2.35 mm) with 4- to 5 1/8- (mean 4 1/2+) tightly coiled whorls, the last descending rapidly in front. Apex and spire (Fig. 128c) flat to slightly elevated, SP/BWW ratio 0.09–0.27 (mean 0.18), height 0.95–1.83 mm (mean 1.30 mm). H/D ratio 0.49–0.61 (mean 0.55). Protoconch of 1 1/2 to 1 5/8 whorls, mean diameter 491.8 μm at 1 1/2 whorls. Apical sculpture (Fig. 128f) of widely spaced, slightly curved, broad, prominent radial ribs, and low, inconspicuous spiral cords. Postnuclear sculpture (Fig. 128g) of broad, widely spaced, protractively sinuated radial ribs.

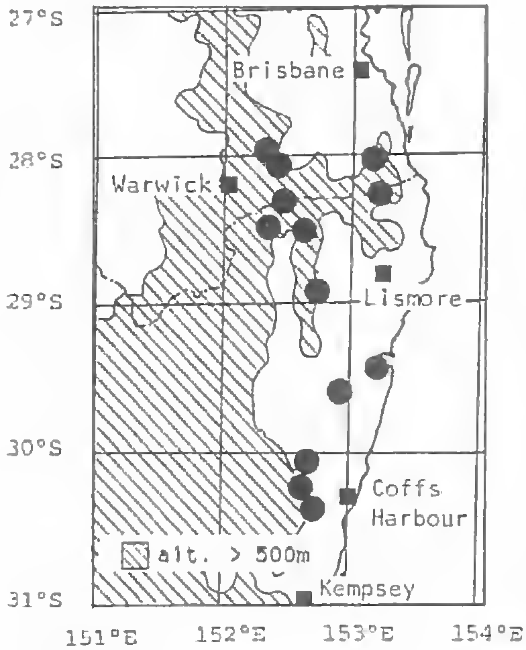


FIG. 130. Distribution of *Egilomen cochlidium* (Cox, 1868).

30–47 (mean 36.8) ribs on the body whorl. Ribs/mm 4.22–5.99 (mean 5.07). Microsculpture (Fig. 128g) of fine radial riblets, 8–12 between each pair of major ribs, and fine crowded spirals. Sculpture continuous on the base. Umbilicus (Fig. 128b) wide to very wide, U-shaped, diameter 0.60–1.03 mm(mean 0.82 mm). D/U ratio 2.59–3.47 (mean 2.93). Sutures impressed. Whorls flattened below and rounded above a laterally compressed periphery (Fig. 128c). Aperture ovately lunate. Lip simple, thick, margins convergent. Columella only slightly dilated. Parietal callus well developed. Colour white to light straw-yellow, often covered in dirt particles. Based on 10 measured adults.

Vas deferens a thin tube. Epiphallus (Fig. 129b), cylindrical, greatly expanded, reflexing prior to entering penis apically through a simple pore surrounded by two fleshy lips. Penis (Fig. 129b) short, internally with a large, apical, longitudinal pilaster, and a basal, circular pilaster. Penial retractor muscle (Fig. 129b) inserted on the epiphallus prior to its junction with the penis. Free oviduct short, muscular, internally with longitudinal pilasters.

Radula (Fig. 128d,h) with central tooth greatly reduced.

Based on two dissected specimens (QMMO16905, QMMO17290).

RANGE AND HABITAT

Mainly confined to cooler subtropical notophyll vine forests on highlands of the Great Dividing Range (between Dorrigo, NSW and the Mistake Mountains, SEQ), and the McPherson Ranges on the NSW/QLD border. The early Grafton/Clarence River records need to be confirmed. The only data available on microhabitat are from a specimen collected from soil under a rock at Canungra, SEQ.

REMARKS

The apical longitudinal penial pilaster and basal penial stimulator contrast with the apical stimulator and basal longitudinal pilaster of *E. globosa*. This difference in penial surface sculpture is probably a species recognition change brought about by sympatric interaction. *E. cochlidium* is poorly represented in collections.

Egilomen globosa sp. nov.
(Figs 131–133; Tables 22, 25)

ETYMOLOGY

Latin *globosa*, rounded; referring to shell shape.

COMPARISONS

E. globosa differs from *E. cochlidium* in having a more globose shell with strongly elevated spire,more crowded radial ribs, more prominent spiral cords and closed umbilicus. *E. globosa* is most apt to be confused with the sympatric *Cralopa stroudensis* (Fig. 95) which has similar shell shape, prominent radial ribbing and closed umbilicus. However, *C. stroudensis* has fewer whorls, a more conspicuous apertural sinus, less elevated spire, thinner lip, and a greater number of ribs on the body whorl. *Elsothera genithecata* (Fig. 108) and *E. nautilodea* (Fig. 106), from northern NSW, have closed umbilici and prominent radial ribs, but are much larger, with flatter spires, and comparatively less crowded radial ribs on the body whorl.

TYPE MATERIAL

HOLOTYPE: QMMO17292, sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ 27°04'S, 152°41'E. Collected 31 Sept 1982, AM/QM - ABRS. Height of shell 1.87 mm, diameter 2.47 mm. H/D ratio 0.76, whorls 4 3/4. PARATYPES: QMMO12178, AMC136521, 20 specimens, same collection data as holotype; Mt

Guyra N.P., SEQ (25°49'S, 152°35'E) MVF/NVF/*Araucaria* (9, QMMO12068, AMC136463, 7 Sept 1982, AM/QM - ABRS); near base, Mt Warning N.P., NSW (28°24'S, 153°16'E) NVF/Palms (2, QMMO-10483, Mar 1981, AM/QM - ABRS); Mt Warning, N.P., NSW (28°24'S, 153°17'E) (3, AMC129305, 19 Mar 1981, AM/QM - ABRS); Natural Bridge N.P., SEQ (28°13'S, 153°14'E) NVF (8, QMMO10459, AMC129270, 18 Mar 1981, AM/QM - ABRS); Terania Creek, Nightcap Range N.P., NSW (28°34'S, 153°19'E), subtropical rainforest, under bark on log (15, QMMO17012, 11 Mar 1987, J. Stanisic, D. Potter; 13, QMMO17148, 11 Apr 1987, J. Stanisic, J. Chaseling).

OTHER MATERIAL

Toonumbar Forest Road, Toonumbar S.F., NSW (28°33'S, 152°45'E) CNVF (1, QMMO10911, 14 Mar 1981, AM/QM - ABRS); Rainforest Park, near Maleny, on Maleny-Montville Rd, SEQ, NVF (1, QMMO11882, 5 Dec 1982, J. Stanisic); sidetrack off Mt Archer Rd, Mt Mee S.F. SEQ (27°04'S, 152°41'E) (2, QMMO15075, QMMO15076, 6 Sept 1983, J. Stanisic, D. Potter; 2, QMMO12177, AMC136520, 30 Sept 1982, AM/QM - ABRS); Fred's Rd, Mt Mee, SEQ (27°05'S, 152°43'E) NVF, litter (1, QMMO-15983, 28 Oct 1984, J. Stanisic, D. Potter); c. 1.6 km N of Numinbah Valley turnoff on Burleigh-Springbrook Rd, SEQ, NVF/Palms, litter (1, QMMO-17293, 17 Dec 1980, J. Stanisic); Kenilworth S.F., SEQ (26°37'S, 152°42'E) rainforest, litter (1, QM-MO17294, 22 May 1980, J. Stanisic, A. Green); Byangum, NSW (1, AMC152199, Lower); Murwillumbah, NSW (1, AMC28495, ex Tech. Mus.); Northern Rivers, NSW (1, AMC63823, Petterd, ex Cox); top of Condamine River Valley, NSW (28°15'S, 152°29'E) (1, AMC128902, 16 Mar 1981, AM/QM - ABRS).

DIAGNOSIS

Shell diameter 1.62–2.47 mm (mean 2.14 mm) of 4 3/8 to 5 (mean 4 5/8+) tightly coiled whorls, last whorl descending more rapidly. Apex and spire (Fig. 131c) moderately to strongly elevated, SP/BWW ratio 0.25–0.55 (mean 0.43), height of shell 1.19–2.04 mm (mean 1.64 mm), H/D ratio 0.71–0.96 (mean 0.77). Protoconch of 1 3/8 to 1 5/8 whorls, mean diameter 497.5 μm at 1 1/2 whorls. Apical sculpture (Fig. 131e) of slightly curved, evenly spaced, broad radial ribs. Postnuclear sculpture (Fig. 131f) of strong, slightly protractively sinuated radial ribs, 53–80 (mean 64.1) ribs on the body whorl. Ribs/mm 7.75–12.19 (mean 9.04). Rib interstices about 4–5 times their width. Microsculpture (Fig. 131f) of thread-like radial riblets crossed by low, crowded spiral cords. Umbilicus closed or reduced to a lateral crack. Sutures impressed; whorls slightly shouldered above and rounded below a laterally compressed periphery. Aperture roundly lunate. Lip expanded at the basal and columellar margins, occasionally with a basal denticle. Columella strongly dilated with a ridge-like thickening, reflected over the umbilicus. Lip sinuous, retracted at the suture to form an apertural sinus. Parietal callus strongly developed. Colour white to light straw-yellow. Based on 14 measured adults.

Genitalia with a strongly expanded, muscular epiphallus (Fig. 132b). Epiphallus with ascending arm parallel to the penis and reflexed before entering the penis apically. Penial retractor muscle (Fig. 132b) inserted on the epiphallus prior to its junction with the penis. Penis (Fig. 132b) internally with a apical longitudinal spongy pilaster and a basal pad-like thickening.

Radula (Fig. 131d,h) similar to *E. cochlidium*.

Based on 6 dissected specimens (QMMO-17012, QMMO17148).

RANGE AND HABITAT

Warm, moist notophyll vine forests of the Big Scrub area, NSW and the D'Aguilar Range, SEQ. It is sympatric with *E. cochlidium* in the McPherson Ranges. An outlier population at Mt Guyra, north of Gympie, SEQ, is the northern limit of the species. *E. globosa* lives under logs.

REMARKS

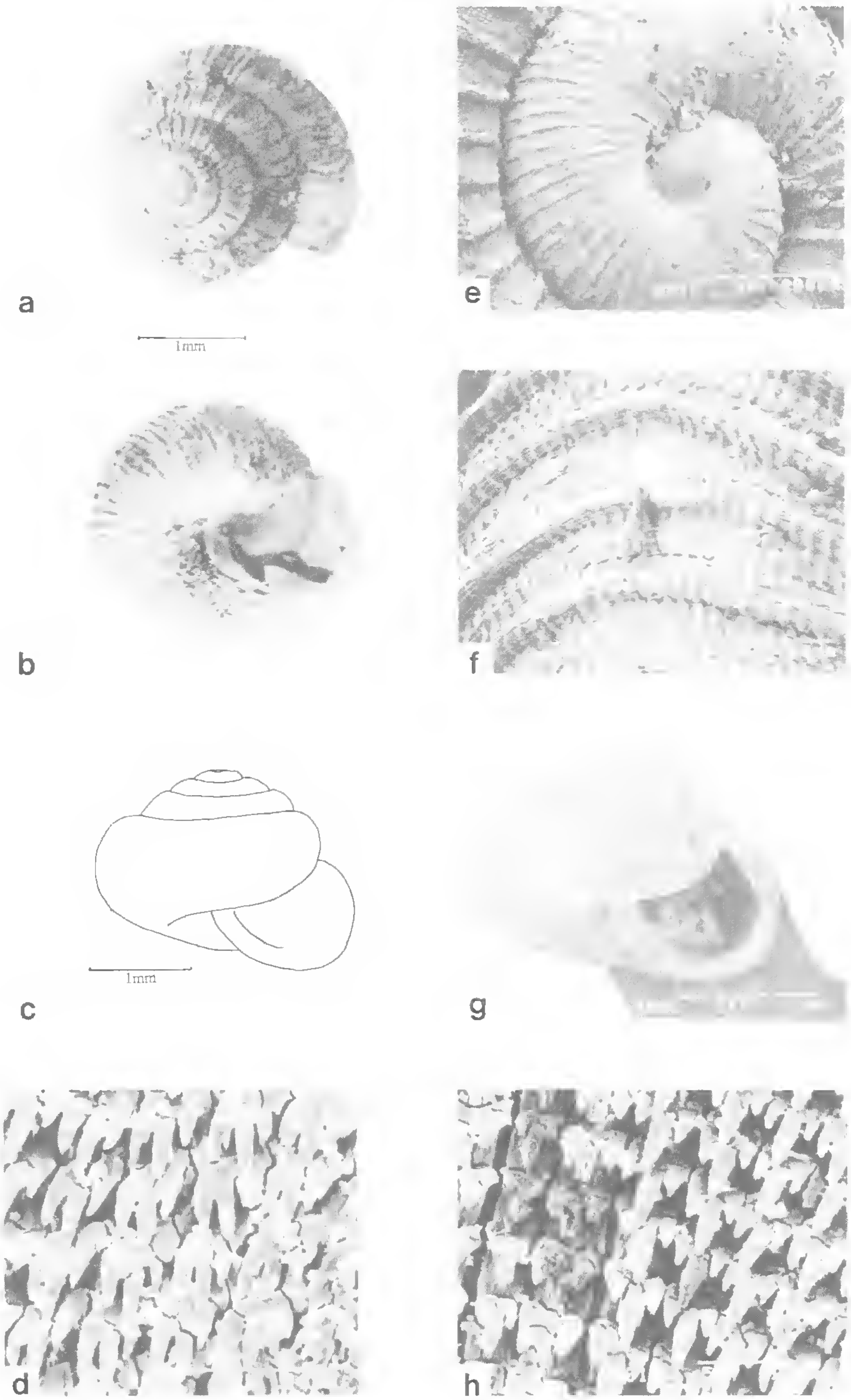
Specimens of *E. globosa* (QMMO12068, AM-C136463) from Mt Guyra are smaller than average and have an altered lip with a small baso-columellar thickening.

Omphaloropa gen. nov.

ETYMOLOGY

From the Greek *omphalos*, umbilicus; referring to the prominent umbilicus.

FIG. 131. *Egilomen globosa* sp. nov. a–c, Sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ. QMMO17292, holotype; d, h, Terania Ck, NSW. QMMO17148, paratype; e-f, Mt Mee S.F., SEQ. QMMO12178, paratype; Mt Guyra N.P., SEQ. QMMO12068, paratype. a-c, entire shell; d, marginal teeth; e, apical sculpture; f, post nuclear sculpture; g, entire shell showing denticle on lip; h, central and lateral teeth. Scale lines as marked.


a
e
1mm
b
f
1mm
c
g
d
h

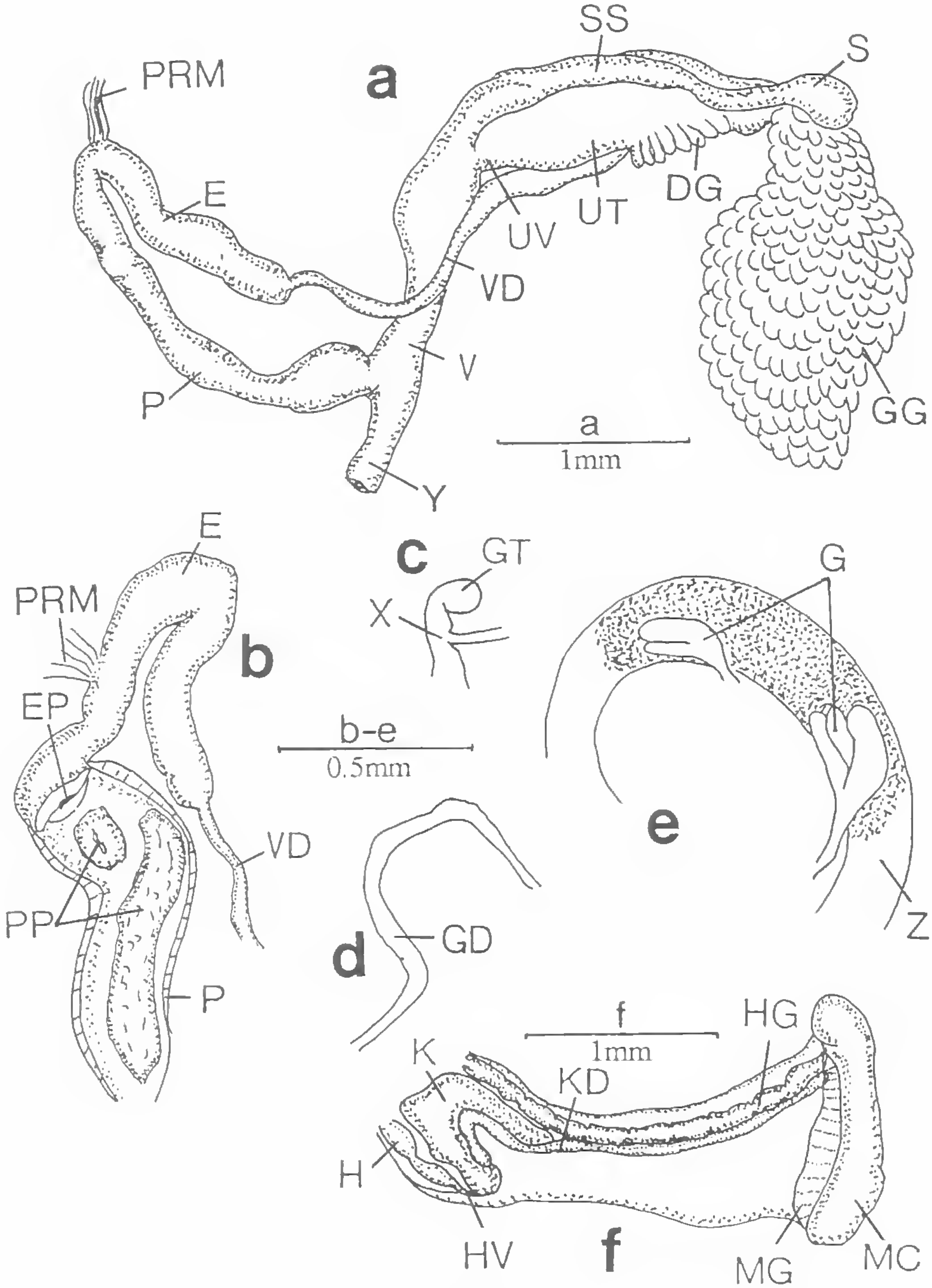


FIG. 132. *Egilomen globosa* sp. nov. Terania Ck, Nightcap Range, N.P., NSW. QMMO17012, paratype. a, genitalia; b, penis interior; c, talon and carrefour; d, hermaphroditic duct; e, ovotestis; f. pallial cavity. Scale lines as marked.

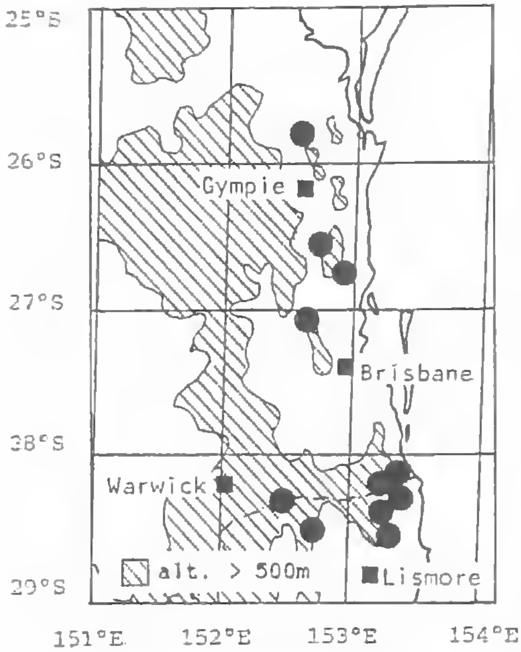


FIG. 133. Distribution of *Egilomen globosa* sp. nov.

TYPE SPECIES
Omphaloropa varicosa sp. nov.

DIAGNOSIS
Shell small, mean diameter 2.23 mm, with tightly coiled whorls (mean 4 1/2-), last descending rapidly. Apex and spire moderately elevated. Protoconch with low spiral cords. Post nuclear sculpture of very widely spaced, prominent, protractively sinuated radial ribs and microsculpture of low radial riblets and spiral cords which have raised knobs at their intersection. Umbilicus wide, cup-shaped. Sutures strongly impressed. Aperture roundly lunate, lip simple. Columella only slightly dilated.

Terminal male genitalia with epiphallus poorly differentiated from vas deferens, entering penis apically through a papillate verge. Penis with a sheath and internal longitudinal pilasters. Female genitalia without unusual features. Radula with very small tricuspid central tooth, otherwise typical.

COMPARISONS
Omphaloropa is conchologically distinguished by small size, apical spiral cords, few widely spaced radials on the adult whorls and wide cup shaped umbilicus. *Rhophodon* is also small, with wide umbilicus and many to few radial ribs on the adult whorls, but in contrast has curved, spaced radials on the protoconch, and few to many lamellate barriers in the aperture. *Sinployea intensa* has a spirally lirate protoconch but more crowded postnuclear radial ribs.

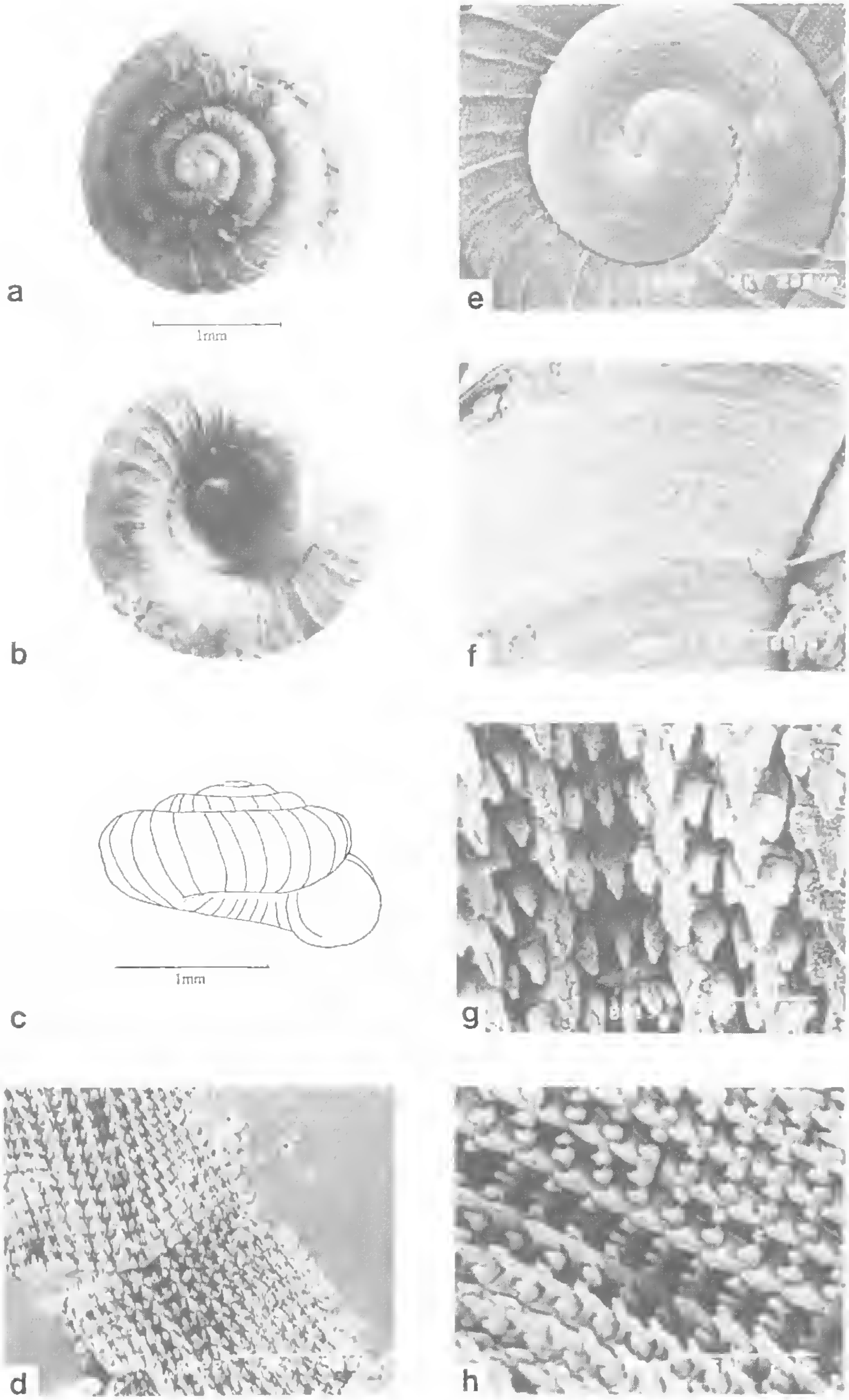
Omphaloropa varicosa sp. nov.
(Figs 134–136: Tables 26, 27)

ETYMOLOGY
Latin *varix*, dilated vein; referring to the prominent postnuclear radial ribs.

COMPARISONS
Within its range, *O. varicosa* is most apt to be confused with *Sinployea intensa* and species of *Rhophodon*. *S. intensa* has a brown shell with spiral cords on the protoconch but has very crowded radial ribs on the body whorl and much smaller umbilicus (Fig. 137). Sympatric *Rhophodon* also have monochrome or flammulated shells with wide umbilicus and few to many radial ribs on the adult whorls. However, in contrast to *O. varicosa*, they have a radially lirate protoconchs with weak spiral elements, and few to numerous apertural lamellae.

TYPE MATERIAL
HOLOTYPE: QMMO17281, Gavial Creek, Bouldercombe, SEQ (23°34'S, 150°28'E) MVF, in litter, collected by J. Stanisic, D. Potter, 9 Jul 1983. Height of shell 1.42 mm, diameter 2.36, H/D ratio 0.60, D/U ratio 2.21, whorls 4 5/8.
PARATYPES: SOUTH-EAST QUEENSLAND - QMMO16805, 88 specimens, same data as holotype; sidetrack off Mt Archer Rd, Mt Mee S.F., (27°04'S, 152°41'E) NVF/Araucaria (3, QMMO15077, 6 Sept 1983, J. Stanisic, D. Potter); Dawes Range (24°28'S, 151°07'E) MVF/Araucaria (600+, QMMO12671, AMC136800; AMC136780 QMMO12651, 4 Sept 1982, AM/QM-ABRS); Bouldercombe Falls, SEVT (2, QMMO17279, 29 Mar 1983, G. Annabell); Dan Dan Scrub, SEVT, in litter (5, QMMO16803, 10 May 1984, J. Stanisic, D. Potter); Freds Rd, Mt Mee (27°05'S, 152°43'E), rainforest, leaf litter (7, QMMO-8363, 14 Apr 1980, J. Stanisic, N. Hall, A Green); Kenilworth S.F. (26°40'S, 152°36'E) *Araucaria*, leaf litter (15, QMMO17280, 22 May 1980, J. Stanisic, A. Green).

OTHER MATERIAL
SOUTH-EAST QUEENSLAND - Entrance to state forest off Yabba Creek Rd, Yabba Creek S.F. (26°28'S, 152°38'E) (1, QMMO13370, 7 Sept 1982,


a
1mm
e
b
f
1mm
c
g
d
h

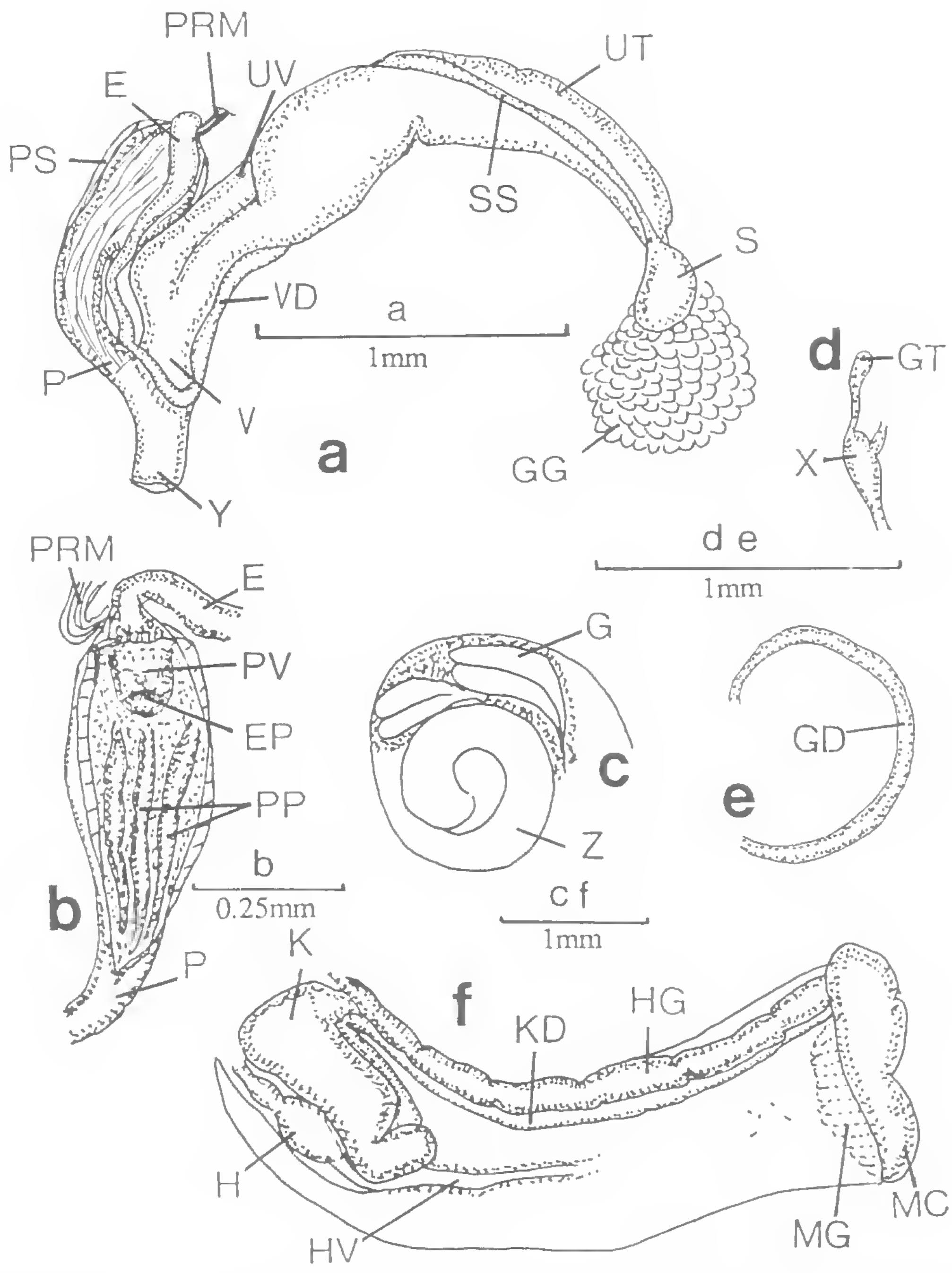


FIG. 135. *Omphaloropa varicosa* sp. nov. Gavial Ck, Bouldercombe, SEQ. QMMO16805, paratype. a, genitalia; b, penis interior; c, ovotestis; d, talon; e, hermaphroditic duct; f, pallial cavity. Scale lines as marked.

FIG. 134. *Omphaloropa varicosa* sp. nov. a–c, Gavial Creek, Bouldercombe, SEQ. QMMO17281, holotype; d–h, same data as holotype, QMMO16805, paratypes. a–c, entire shell; d, radula; e, apical sculpture; f, post nuclear sculpture; g–h, central and lateral teeth. Scale lines as marked.

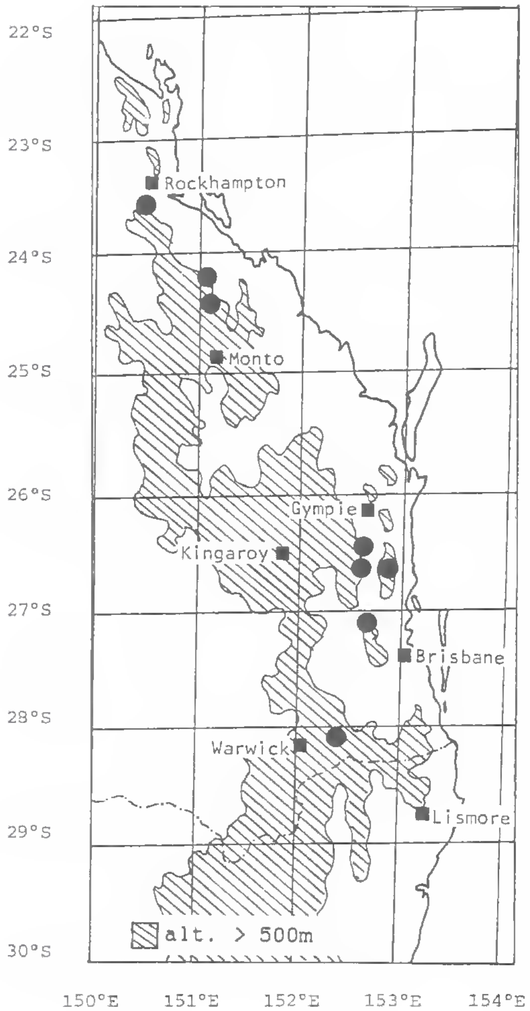


FIG. 136. Distribution of *Omphaloropa varicosa* sp. nov.

AM/QM-ABRS); Fred's Rd, Mt Mee (27°05'S, 152°43'E) NVF, litter (1, QMMO15981, 28 Oct 1984, J. Stanisic, G. Annabell); Cunningham's Gap, near monument (28°04'S, 152°24'E) 755m, SNVF/ferns (8, AMC136808, QMMO12679, 7 Dec 1981, AM/QM-ABRS); Little Yabba Ck, Imbil S.F. (26°28'S, 152°38'E) NVF (6, QMMO12020, AMC136437, 8 Sept 1982, AM/QM-ABRS); Montville Rd, near Kondalilla Falls N.P. (26°40'S, 152°52'E) vine thicket on side of road (1, QMMO-11979, 8 Sept 1982, AM/QM-ABRS).

DIAGNOSIS

Shell diameter 2.03–2.34 mm (mean 2.23 mm) with 3 3/4 to 4 3/4 (mean 4 1/2-) tightly coiled whorls last descending rapidly. Apex and spire (Fig. 134c) moderately elevated, SP/BWW ratio 0.18–0.44 (mean 0.29), height 1.03–1.42 mm (mean 1.26 mm). H/D ratio 0.50–0.64 (mean 0.7). Last whorl descending more rapidly. Protoconch white, glossy, exsert, 1 1/2 to 1 3/4 whorls, mean diameter 505.1 μm at 1 1/2 whorls. Apical sculpture (Fig. 134e) of 12–15 low spiral cords. Postnuclear sculpture (Fig. 134a) of widely spaced, prominent, protractively sinuated radial ribs, 18–35 (mean 26.8) ribs on body whorl. Ribs/mm 2.79–4.93 (mean 3.83). Microsculpture (Fig. 134f) of fine thread-like radial riblets, 18–35 between each pair of major ribs, crossed by numerous low spiral cords with distinct raised knobs produced at their intersection. Umbilicus (Fig. 134b) wide, cup-shaped, diameter 0.70–1.07 mm (mean 0.91 mm), D/U ratio 2.16–2.92 (mean 2.48). Sutures strongly impressed. Whorls rounded below and shouldered above a rounded periphery (Fig. 134c). Aperture roundly lunate. Lip simple, thickened slightly. Columella only slightly dilated. Parietal callus strongly developed. Colour brown with alternate light and dark brown radial streaks. Based on 29 measured adults.

Genitalia with a poorly differentiated epiphallus which enters the penis apically through a large papilla (Fig. 135a,b). Penial retractor muscle inserting on the penis adjacent to the penis-epiphallus junction. Epiphallus internally with longitudinal pilasters. Penis (Fig. 135b) pear-shaped with a distinct bulb and sheath, internally with apical papilla and low, spongy longitudinal pilasters.

Based on 3 dissected specimens (QMMO-15077, QMMO16805).

RANGE AND HABITAT

Humid subtropical notophyll vine forests in the southern part of its range; drier microphyll vine forests (with *Araucaria* emergents) and semi-evergreen vine thickets in the north. *O. varicosa* has been found living among litter and in soil, but not under logs.

REMARKS

Conchologically *O. varicosa* could be linked with *Sinployea* but the simple internal penial structures relate *O. varicosa* to other charopids reviewed in this study.

O. varicosa may be abundant in certain localities e.g. 600+ specimens were collected in

TABLE 26. RANGE OF VARIATION IN *OMPHALOROPA, SINPLOYEA* AND *ROTACHAROPA* (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Rotacharopa annabelle	10	5 3/4 (5 3/8–6 1/8)	1.28 (1.13–1.54)	2.00 (1.77–2.36)	0.63 (0.52–0.69)	0.13 (0.08–0.23)	0.82 (0.72–0.95)	0.16 (0.11–0.26)	41.3 (34–51)	6.62 (5.60–7.43)	0.25 (0.23–0.27)	7.66 (6.85–8.54)
Rotacharopa kessneri	18	5+ (4 7/8–to 5 5/8+)	1.31 (1.15–1.60)	2.15 (1.95–2.46)	0.61 (0.57–0.65)	0.12 (0.08–0.21)	0.86 (0.76–1.05)	0.15 (0.10–0.24)	95.8 (57–146)	14.19 (8.83–19.32	0.23 (0.16–0.29)	9.71 (7.23–11.90)
Rotacharopa densilamellata	14	5 1/8+ (4 5/8–to 5 7/8–)	1.35 (1.23–1.52)	1.94 (1.79–2.16)	0.71 (0.67–0.78)	0.27 (0.16–0.39)	0.79 (0.72–0.90)	0.34 (0.21–0.53)	139 (93–206)	27.10 (16.18–36.68)	0.41 (0.36–0.51)	4.93 (4.08–5.27)
Omphaloropa varicosa	29	4 1/2– (3 3/4–4 3/4)	1.26 (1.03–1.42)	2.23 (2.03–2.36)	0.57 (0.50–0.64)	0.20 (0.12–0.29)	0.68 (0.58–0.74)	0.29 (0.18–0.34)	26.80 (18–35)	3.83 (2.79–4.93)	0.91 (0.70–1.07)	2.48 (2.16–2.92)
Sinployea intensa	17	3 5/8+ (3 1/2 to 3 7/8+)	1.13 (0.97–1.31)	2.31 (1.95–2.55)	0.50 (0.45–0.54)	0.08 (0.02–0.12)	0.71 (0.66–0.84)	0.12 (0.02–0.19)	92.1 (81–116)	13.11 (10.65–16.79)	0.66 (0.55–0.78)	3.48 (3.17–4.00)

the Dawes Range, SEQ (QMMO12671, QMMO12651, AMC136800, AMC136780) in September, 1982.

Sinployea Solem, 1983

Sinployea Solem, 1983, p.81.

Type Species

Sinployea peasei Solem, 1983; by original designation.

Previous Studies

Solem (1983) introduced *Sinployea* for 49 Pacific Island charopids that show a uniform pattern of anatomical variation. The penis interior is characterised by an apical verge, muscular collar and stimulatory pads in the lower part of the chamber. Conchologically *Sinployea* is conservative with fine apical spiral cords, rounded whorls with radial ribs, and microsculpture of radial riblets and fine, low spiral cords in all species.

Sinployea includes '*Cralopa*' *intensa* Iredale, 1941, whose characters are close to the average Pacific Island species.

Distribution and Ecology

In the Marianas in Micronesia; parts of Melanesia including Kiribati (= Solomon Is) and Vanuatu (= New Hebrides); and into Polynesia as far east as the Society Islands. Locally *S. intensa* is confined to subtropical notophyll vine forests of northern NSW and SEQ. Its northern limit is the Rundle Range near Rockhampton. *S. intensa* often occurs in strand-line rainforests within this region e.g. at Byron Bay, NSW; Cooloola, SEQ; Eurimbula, near Bundaberg, SEQ; and Burleigh Heads, SEQ.

Comparisons

Sinployea is not easily confused with other Charopidae. The small, reddish-brown shell, slightly elevated spire, apical spiral cords and postnuclear crowded radial ribs are distinctive. *Setomedea* is larger, has apical spiral cords, and more complex adult sculpture with periostracal setae on the major ribs. *Cralopa* has prominent radial ribs, narrow to closed umbilicus, apertural sinus, and apical sculpture of low, broad, radial ribs and weak, low spiral cords. *Omphaloropa* (Fig. 134), has apical spiral cords but few major radials on the body whorl, a wide cup-shaped umbilicus, and low microsculpture.

TABLE 27 - LOCAL VARIATION IN *OMPHALOROPA VARICOSA* SP. NOV. (MEAN AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Omphaloropa varicosa												
Bouldercombe												
QMMO 17281 (Holotype)	1	4 5/8	1.42	2.36	0.60	0.23	0.72	0.31	29	3.91	1.07	2.21
QMMO 17279	1	4 3/8+	1.17	2.16	0.54	0.21	0.66	0.31	32	4.72	0.90	2.39
Dawes Range												
QMMO 12651	2	4 5/8+	1.33±0.095 (1.23–1.42)	2.21±0.025 (2.18–2.22)	0.61±0.035 (0.57–0.64)	0.20±0.035 (0.16–0.23)	0.68±0.020 (0.66–0.70)	0.29±0.035 (0.25–0.32)	--- ---	--- ---	0.84±0.020 (0.82–0.86)	2.61±0.040 (2.57–2.65)
QMMO 12671	10	4 5/8- (4 3/8+to4 3/4)	1.28±0.029 (1.15–1.42)	2.26±0.042 (2.12–2.36)	0.56±0.031 (0.51–0.64)	0.21±0.013 (0.16–0.29)	0.69±0.007 (0.66–0.72)	0.31±0.018 (0.23–0.42)	30.3±1.19 (25–35)	4.31±0.173 (3.55–4.93)	0.85±0.016 (0.76–0.92)	2.61±0.045 (2.40–2.92)
Kenilworth S.F.												
QMMO 17280	3	4- (3 3/4–4+)	1.13±0.050 (1.03–1.19)	2.04±0.007 (2.03–2.05)	0.55±0.027 (0.50–0.59)	0.13±0.013 (0.12–0.16)	0.64±0.031 (0.58–0.68)	0.22±0.035 (0.18–0.29)	19.0±0.58 (18–20)	2.95±0.090 (2.79–3.10)	0.73±0.018 (0.70–0.76)	2.80±0.061 (2.70–2.91)
Mt Mee												
QMMO 8363	1	4 1/8+	1.23	2.28	0.54	0.16	0.74	0.22	21	2.93	0.82	2.78
QMMO 16805	11	4 5/8+ (4 1/8–4 5/8)	1.26±0.030 (1.21–1.34)	2.28±0.015 (2.20–2.36)	0.56±0.008 (0.51–0.59)	0.21±0.013 (0.16–0.29)	0.67±0.006 (0.64–0.70)	0.31±0.018 (0.24–0.44)	26.4±1.48 (21–33)	3.72±0.204 (3.01–4.65)	1.01±0.013 (0.90–1.03)	2.26±0.024 (2.16–2.46)

Sinployea intensa (Iredale, 1941)
(Figs 137–139; Tables 26, 28)

Cralopa intensa Iredale, 1941a, p. 269, fig. 5.

Comparisons

S. intensa is distinguished from sympatric charopids by its small brown shell which has few whorls, small umbilicus, apical spiral cords, and postnuclear sculpture of crowded, protractively sinuated radial ribs. *Setomedea nudicostata* (Fig. 35) has a flammulated shell and squiggly apical spiral cords. *Omphaloropa varicosa* (Fig. 134) has a brown to flammulated shell with few prominent radial ribs. *Discocharopa aperta* (Fig. 93) has crowded radial ribs on adult whorls but is smaller, white to straw-yellow in colour, with wide umbilicus, radially lirate apex, and complex postnuclear spiral sculpture.

Type Material

Holotype: AMC63496, Bryon Bay, NSW. Height 1.15 mm, diameter 2.30 mm, H/D ratio 0.50. D/U ratio 4.00, whorls 3 5/8+.

Other Material

AMC31650, AMC63769, 4 specimens, Cape Byron, NSW. Collected Lower, ex J.C. Cox; Kenilworth S.F., SEQ (26°37'S, 152°42'E) rainforest, leaf litter (1, QMMO17284, 22 May 1980, J. Stanisic, A. Green); Mt Mudlo, Kilkivan S.F., SEQ (26°01'S, 152°13'E) *Araucaria*/NVF, litter (13, QMMO17283, 17 Jul 1980, J. Stanisic, A. Green); Kalpowar S.F., SEQ (24°43'S, 151°21'E) MVF/Araucaria, litter (12, QMMO17287, 15 Jul 1980, J. Stanisic, A. Green); rainforest walk, Kalpowar S.F., SEQ (24°41'S, 151°21'E) MVF/*Araucaria* (1, QMMO12576, 4 Sept 1982, AM/QM-ABRS); Below summit, Mt Warning, NSW (28°24'S, 153°16'E) (1, QMMO10511, Mar 1981, AM/QM-ABRS); Mt. Fort William, Kalpowar S.F., SEQ, 833 m, CNVF (1, QMMO16824, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton); Whian Whian S.F. N. of Lismore, NSW, rainforest (1, QMMO6294, 12 Sept 1976, M.J. Bishop); Mt Guyra N.P., SEQ (25°49'S, 152°35'E) MVF/NVF/*Araucaria* (2, QMMO12075, 7 Sept 1982, AM/QM-ABRS); Burleigh Heads N.P., SEQ, vine thicket, under logs (2, QMMO16917, 21 Jan 1987, J. Stanisic, D. Potter); Freds Road, Mt Mee SEQ (27°05'S, 152°43'E) NVF, litter (1, QMMO15980, 28 Oct 1984, J. Stanisic, G. Annabell); Cooloola N.P., SEQ (25°55', 153°08'E) 50m, CNVF on sand (1, QMMO6350, 25 Oct 1976, M.J. Bishop); sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ (27°04'S, 152°41'E) (1, QMMO12180, 31 Sept 1982, AM/QM-ABRS; Byangum, Tweed River dis-

TABLE 28. LOCAL VARIATION IN *SINPLOYEA INTENSA* (IREDALE, 1941) (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Sinployea intensa												
Byron Bay												
AMC63106 (Holotype)	1	3 5/8+	1.15	2.30	0.50	0.08	0.80	0.10	93	12.86	0.58	4.00
AMC63709	2	3 3/4-	1.07±0.021 (1.05–1.09)	2.35±0.010 (2.34–2.36)	0.46±0.005 (0.45–0.46)	0.05±0.010 (0.04–0.06)	0.70±0.021 (0.68–0.72)	0.08±0.02 (0.06–0.09)	88.00±5.00 (83–93)	11.91±0.73 (11.18–12.63)	0.64±0.021 (0.62–0.66)	3.70±0.135 (3.56–3.83)
AMC31650	1	3 5/8	1.13	2.28	0.50	0.12	0.68	0.18	---	--	0.64	3.58
Mudlo Gap QMMO 12352	2	3 3/4	1.25±0.021 (1.23–1.27)	2.46±0.082 (2.38–2.55)	0.51±0.03 (0.48–0.53)	0.62±0.041 (0.02–0.10)	0.80±0.041 (0.76–0.84)	0.08±0.06 (0.02–0.14)	94	11.74	0.73±0.010 (0.72–0.74)	3.38±0.07 (3.31–3.45)
Benarkin QMMO 12239	1	3 3/4+	1.15	2.36	0.49	0.12	0.73	0.17	97	13.06	0.72	3.28
Mt Gayta QMMO 12075	1	3 1/2+	0.97	2.01	0.48	0.12	0.66	0.19	96	15.17	0.55	3.63
Colosseum Creek QMMO 13264	1	3 1/2+	1.05	1.95	0.54	0.06	0.66	0.09	92	15.00	0.62	3.17
Kalpowar S.F. QMMO 12287	5	3 3/4- (3 1/2–3 7/8-)	1.16±0.048 (1.07–1.31)	2.36±0.087 (2.16–2.57)	0.49±0.01 (0.46–0.52)	0.09±0.008 (0.06–0.10)	0.71±0.026 (0.66–0.78)	0.13±0.01 (0.09–0.16)	83.50±1.19 (81–86)	11.53±0.30 (10.65–11.90)	0.69±0.031 (0.64–0.78)	3.41±0.04 (3.20–3.50)
QMMO 12576	1	3 5/8	1.11	2.20	0.50	0.10	0.66	0.16	116	16.79	0.64	3.45
Bobby Range QMMO 12141	2	3 5/8- (3 5/8 to 3 5/8)	1.10±0.011 (1.09–1.11)	2.09	0.53±0.005 (0.52–0.53)	0.09±0.011 (0.08–0.10)	0.70	0.14±0.02 (0.12–0.15)	95.50±2.50 (93–98)	14.50±0.38 (14.12–14.88)	0.62	3.40

trict, Nth NSW, scrub, (2, AMC63779); Cape Byron, Nth NSW, (2, AMC140493, 1 May 1958, L. Price); Byron Bay, NSW (2, AMC140483, C.F. McLauchlan); South Grafton, NSW (2, AMC.63785); Mudlo Gap, Mudlo S.F., SEQ, MVF/Araucaria, (26°01'S, 152°14'E), (55, AMC136654, QMMO-12352, 2 Oct 1982, AM/QM-ABRS); Yarraman Forest Drive, Yarraman S.F., SEQ, MVF, (26°50'S, 151°57'E), (3, AMC136587, QMMO12262, 31 Sept 1982, AM/QM-ABRS); Cooloola Nat. Park, SEQ, SNVF on sand (25°57'S, 153°06'E) (2, AMC136489, QMMO12112, 6 Sept 1982, AM/QM-ABRS); Bobby Range S.F. SEQ, NVF, (24°37'S, 151°32'E) (10, AMC136505, QMMO12141, 6 Sept 1982, AM/QM-ABRS); Blackbutt Range, c. 7.4 km S of Benarkin, SEQ, MVF/Araucaria (26°53'S, 152°11'E), (5, AMC136565, QMMO12239, 31 Sept 1982, J. Stanisic, D. Potter); Mt Fort William, Kalpowar SF, SEQ, NVF (24°39'S, 151°20'E) (2, AMC136759 QMMO12690, 4 Sept 1982, AM/QM-ABRS); NE of Monto, Kalpowar SF., SEQ, vine thicket/scrub litter (24°42'S, 151°21'E) (2, AMC137851, QMMO13153, 4 Sept 1982, AM/QM - ABRS); NW of Miriam Vale, Colosseum Ck., SEQ, rainforest along creek (24°23'S, 151°27'E) (7, AMC137894, QMMO13264, 6 Sept 1982, AM/QM-ABRS); Bulburin SF, S of Gladstone, SEQ, 540 m, CNVF-A1 forest type (24°31'S, 151°29'E) (1, AMC152213, 8 May 1975, W.F. Ponder, J.B. Burch, P.H. Colman); Eurimbula S.F., S of Gladstone, SEQ, 10 m (24°11'S, 151°50'E) (4, AMC152214, AMC152215, 7 May 1975, J.B. Burch, W.F. Ponder, P.H. Colman); Rundle Range, SE of Rockhampton, SEQ, 30 m (23°39'S, 150°59'E) (many, AMC 152216, AMC152217 6 May 1975, J.B. Burch, W.F. Ponder, P.H. Colman).

DIAGNOSIS

Shell diameter 1.95–2.55 mm (mean 2.31) with 3 1/2+ to 3 7/8- (mean 3 5/8+) loosely coiled whorls, last whorl descending more rapidly. Apex and spire (Fig. 137c) flat to slightly elevated, SP/BWW ratio 0.02–0.19 (mean 0.12), height of shell 0.97–1.31 mm (men 1.13 mm), H/D ratio 0.45–0.54 (mean 0.50). Protoconch of 1 3/8 to 1 1/2 whorls, mean diameter 574.8 μm at 1 1/2 whorls, sometimes exsert but generally flattened. Apical sculpture (Fig. 137d) of c. 12 glossy, evenly spaced, fine spiral cords. Postnuclear sculpture (Fig. 137e) of complex, protractively sinuated, crowded radial ribs, 81–116 (mean 92.1) ribs on the body whorl. Ribs/mm 10.65–16.79 (mean 13.11). Microsculpture (Fig. 137e) of fine radial riblets, 5–11 between each pair of major ribs, and low spiral cords which form raised knobs at their intersec-

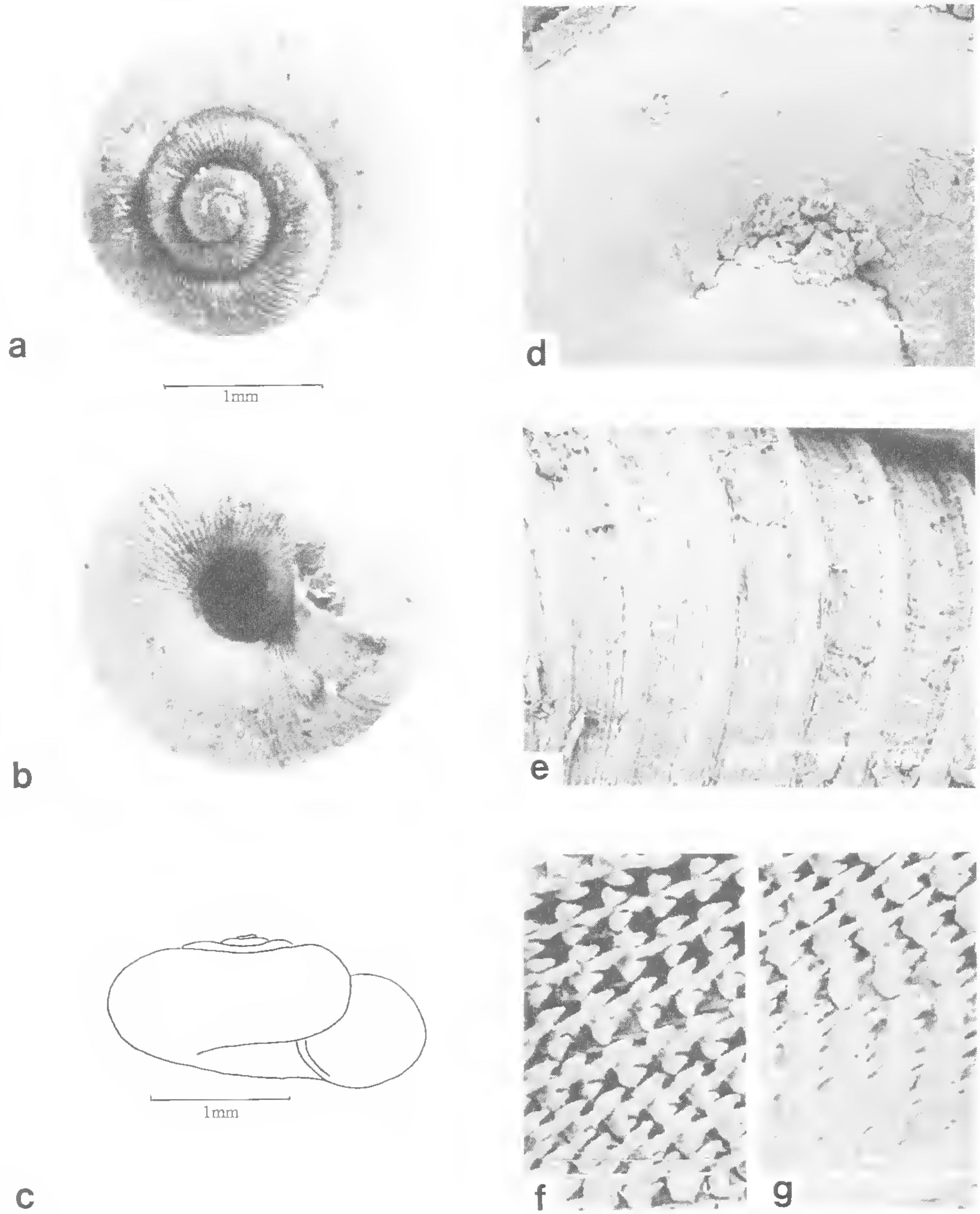


FIG. 137. *Sinployea intensa* (Iredale, 1941). a–c, Bryon Bay, NSW. AMC63496, holotype; d–e, Mudlo Gap, Mudlo S.F., SEQ. QMMO12352; f–g, Cherry Tree North S.F., via Casino, NSW. AMC154769. a–c, entire shell; d, apical sculpture; e, post nuclear sculpture; f, central and lateral teeth; g, marginal teeth. Scale lines as marked.

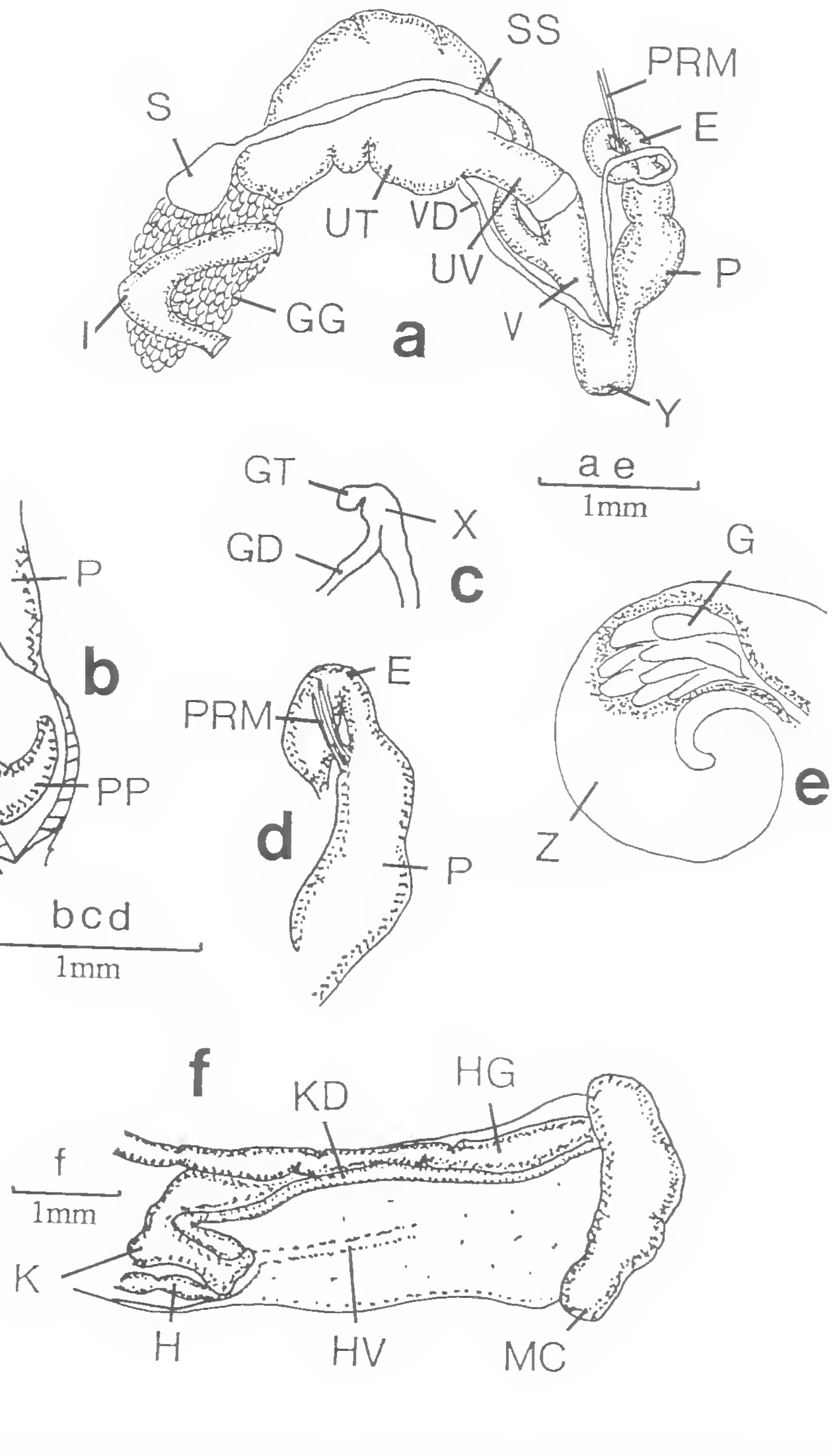


FIG. 138. *Sinployea intensa* (Iredale, 1941). Burleigh Heads N.P., SEQ. QMMO16917. a, genitalia; b, d, details of penis; c, talon and carrefour; e, ovotestis; f, pallial cavity. Scale lines as marked.

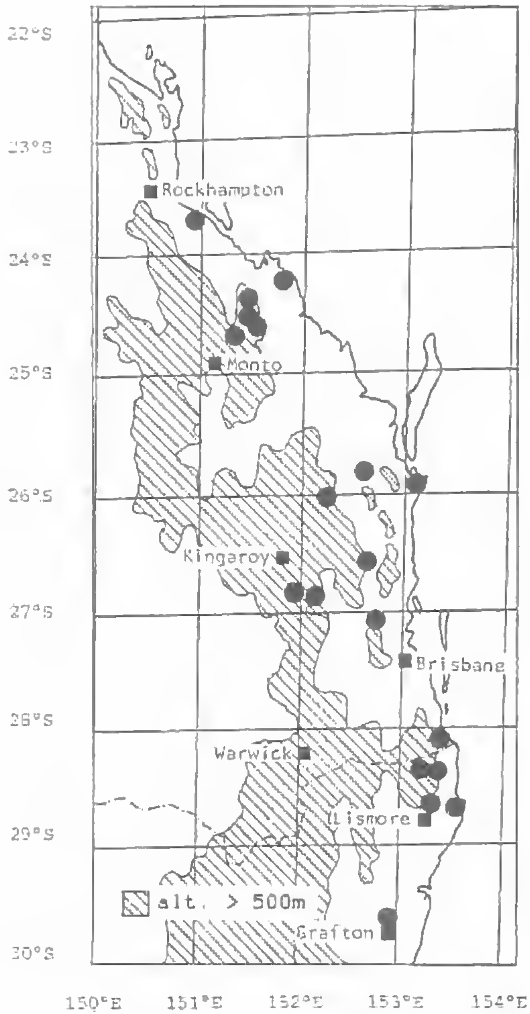


FIG. 139. Distribution of *Sinployea intensa* (Iredale, 1941).

tion with the microradials. Sculpture continuous on the base. Umbilicus (Fig. 137b) wide, V-shaped, last whorl decoiling more rapidly, diameter 0.55–0.78 mm (mean 0.66 mm). D/U ratio 3.17–4.00 (mean 3.78). Sutures strongly impressed. Whorls rounded above and below the periphery (Fig. 137c). Aperture roundly lunate. Lip simple, slightly thickened. Columella weakly twisted toward umbilicus. Parietal callus well developed, margins convergent. Colour brown. Based on 17 measured adults.

Epiphallus (Fig. 138d) short, muscular, reflexing before entering the penis apically, internally with longitudinal pilasters. Penis (Fig. 138a) short; externally differentiated into an upper and a lower chamber; without sheath. Details of upper chamber and epiphallus entry unavailable. Lower chamber with a semicircular (horseshoe-shaped?) pilaster (Fig. 138b). Penial retractor muscle (Fig. 138a) inserting on the penis adjacent to the epiphallus-penis junction.

Radula (Fig. 137f,g) typical for genus.

Based on 1 dissected adult (QMMO16917).

RANGE AND HABITAT

Humid sub-tropical notophyll vine forest in northern NSW and SEQ; drier microphyll vine forest between Gympie and Rockhampton, SEQ; and strand line vine forests at Bryon Bay, NSW, Burleigh Heads, Cooloola and Eurimbula, SEQ. The latter habitat preference is unusual in the context of Australian species but as a remnant of a much wider Pacific Island distribution it is not unexpected. *S. intensa* lives under the bark of fallen trees and has the typical grey markings also present in semi-arboreal Pacific Island *Sinployea*.

REMARKS

S. intensa is similar to *S. euryomphala* (Solem, 1959) from Vanuatu in external appearance of penis, insertion of penial retractor muscle, shape of epiphallus, unusual muscular collar on the free oviduct, and pallial configuration (Solem, 1983). However *S. intensa* has more postnuclear ribs, is smaller in size, and has a less elevated spire.

Subfamily ROTADISCINAE Baker, 1927

This taxon was introduced (Baker, 1927) for endodontoid snails with incomplete secondary ureter, and kidney with a rectal lobe much longer than pericardial lobe. Solem (1983, p. 70) included the subfamily in the Charopidae for species with or without a complete secondary ureter and weakly to strongly bilobed kidney. He considered that the peculiar apical sculpture and unusual variations in genital morphology were the main distinguishing features and included the Northern Hemisphere *Rotadiscus* Pilsbry, 1926, *Radiodiscus* Pilsbry and Ferriss, 1906, *Radioconus* H.B. Baker, 1927 and *Radiodomus* H.B. Baker, 1930, together with *Microcharopa* Solem, 1983 from the Pacific region.

Rotacharopa gen. nov.

ETYMOLOGY

A combination of syllables from Rotadiscinae and Charopidae.

TYPE SPECIES

Rotacharopa annabelli sp. nov.

DIAGNOSIS

Very small to minute Charopidae, diameter range 1.77–2.46 mm, with 4 5/8+ to 6 1/8 very tightly coiled whorls, last descending more rapidly. Apex and spire weakly to moderately elevated. Apical sculpture of short, slightly twisted segments, organised into spiral rows, and weakly curved, low radial ridges. Postnuclear sculpture of very crowded (*densilamellata*) to moderately spaced (*annabelli*), protractively sinuated radial ribs. Microsculpture of very fine radials and low, broad spiral cords which are raised at their intersection with the microradials to form an elongate bead. Umbilicus very narrow, U-shaped to almost completely closed by reflection of the columella. Sutures impressed; whorls shouldered above and rounded below a laterally compressed periphery. Aperture roundly lunate. Parietal callus weakly developed.

Animal with slender foot and tail. Kidney with well developed, vaguely triangular, elongate pericardial lobe and a reduced rectal lobe. Ovotestis two teardrop-shaped lobes lying in the apical whorls of the digestive gland. Terminal male genitalia with epiphallus differentiated into ascending and descending arms. Descending arm of epiphallus with transverse thickenings internally. Epiphallus entering penis through a simple pore surrounded by a large fleshy pilaster. Penial retractor muscle inserted on the epiphallus, or on the epiphallus - vas deferens junction (*annabelli*). Penis large, barrel-shaped, with (*kessneri*), or without a verge, normally with longitudinal pilasters which may be modified (*annabelli*). Penis with short (*annabelli*), long (*kessneri*) to extremely long (*densilamellata*) preputial tubular extension. Vagina long, rarely short (*annabelli*), internally with longitudinal thickenings. Free oviduct short. Atrium without unusual features. Spermatheca typical. Radula with tricuspid central and lateral teeth (central slightly smaller) which have a long slender lanceolate mesocone and short, pointed ectocones.

DISTRIBUTION AND ECOLOGY

Rotacharopa is confined to moist notophyll vine forests and drier microphyll vine forests and vine thickets of south to mid-east Queensland. Undescribed rotadiscines, with flatter shells and more open umbilici, also occur in this region (Stanisic, unpublished). *Rotacharopa kessneri* and *R. annabelli* have been collected in close proximity to each other near Gladstone, SEQ, and further fieldwork may demonstate sympatry. Both species have modified penial surfaces which indicate possible microsympatry but this sympatry may also involve undescribed taxa.

The two southern species, *R. densilamellata* and *R. kessneri* live under logs, whilst *R. annabelli* is a litter dweller.

COMPARISONS

Other charopids reviewed in this study which have similar-sized shells lack the peculiar apical sculpture of *Rotacharopa*. *Rhophodon* has a flattened shell with wide umbilicus, apical sculpture of prominent radial ribs, and apertural barriers; *Discocharopa* has apical sculpture of prominent radial ribs and weak spiral wrinkles, and a saucer-shaped umbilicus; *Omphaloropa* has a very wide cup-shaped umbilicus and continuous spiral cords on the protoconch; and *Sinployea intensa* has continuous apical spiral cords, fewer whorls and a more open umbilicus. *Microcharopa* Solem, 1983 from Fiji is readily distinguished from *Rotacharopa* by its lower whorl count, smaller size, flatter shell and very wide umbilicus.

KEY TO SPECIES OF *ROTACHAROPA*

1. Postnuclear sculpture of widely separate radial ribs (mean ribs/mm 6.62) (Fig. 140a) .... *annabelli*

   Postnuclear sculpture of more crowded radial ribs (Figs 143a, 146a) 2

2. Postnuclear radial ribs very crowded; umbilicus more open (Fig. 146b), mean D/U ratio 4.93 .... *densilamellata*

   Postnuclear radial ribs less crowded; umbilicus more closed (Fig. 143b), mean D/U ratio 9.71 .... *kessneri*

Rotacharopa annabelli sp. nov.
(Figs 140–142; Tables 26, 29)

ETYMOLOGY

For Graeme Annabell who provided assistance with collecting.

COMPARISONS

The widely spaced ribs (mean ribs/mm 6.62),

TABLE 29 LOCAL VARIATION IN *ROTACHAROPA ANNABELLI* SP. NOV. AND *ROTACHAROPA KESSNERI* SP NOV (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Rotacharopa annabelli												
Mt Archer QMMO 17300 (Holotype)	1	6 1/8	1.23	1.89	0.65	0.19	0.76	0.24	41	6.90	0.23	8.36
QMMO 8348	10	5 1/2+ (5 3/8–5 3/4+)	1 15±0.011 (1.13–1.23)	1.86±0.016 (1.77–1.95)	0.62±0.004 (0.60–0.64)	0.10±0.032 (0.08–0.12)	0.77±0.006 (0.72–0.78)	0.14±0.008 (0.11–0.17)	39.0±0.92 (34–44)	6.69±0.144 (5.91–7.20)	0.26±0.004 (0.23–0.27)	7.36±0.124 (6.85–8.00)
Bouldercombe QMMO 16807	4	5 7/8- (5 5/8–6 1/8-)	1.47±0.029 (1.40–1.54)	2.21±0.026 (2.16–2.26)	0.67±0.010 (0.65–0.69)	0.17±0.020 (0.14–0.23)	0.90±0.020 (0.86–0.95)	0.20±0.023 (0.15–0.26)	43 7±3.28 (39–50)	6.33±0.379 (5.75–7.04)	---	...
QMMO 12827	2	5 3/4+ (5 5/8+to5 7/8)	1 43±-.030 (1.40–1.46)	2.26±0.100 (2.16–2.36)	0.64±0.015 (0.62–0.65)	0.16	0.89±0.030 (0.86–0.92)	0.19±0.005 (0.18–0.19)	40.5±2.50 (38–43)	5.70±0.095 (5.60–5.79)	---	---
Mt Morgan QMMO 13117	1	5 5/8	1.34	1.93	0.52	0.10	0.86	0.12	44	7.25	0.23	8.54
Mt Moore QMMO 13203	2	5 7/8	1.49±0 010 (1.48-1.50)	2.19±0.010 (2.18-2.20)	0.68±0.010 (0.67–0.69)	0.17±0.025 (0.14–0.19)	0.94±0.015 (0.92–0.95)	0 18±0.020 (0.16–0.20)	50.5±0.50 (50–51)	7.35±0.105 (7.24–7.45)	...	...
Rotacharopa kessneri												
Kalpowar S.F. QMMO 17302 (Holotype)	1	5 1/4+	1 40	2.28	0.61	0.16	0.86	0.19	67	9.35	0.21	11.12
QMMO 17303	2	4 7/8+ (4 7/8–5)	1.21±0.020 (1.19–1.23)	2.01±0.155 (1.85–2.16)	0.61±0.035 (0.57–0.64)	0.11±0.010 (0.10–0.12)	0.80±0.020 (0.78–0.82)	0.14±0.010 (0.13–0.15)	88.0±15.00 (73–103)	13.88±1.315 (12.56–15.19)	0 22±0.010 (0.21–0.23)	9.28±0.265 (9 01–9.54)
Limestone Creek QMMO 13127	1	4 7/8-	1.15	1.89	0 61	0.08	0.76	0.11	90	15.15	0 19	10.21
Cania QMMO 17305	1	5 1/2+	1.44	2.42	0.59	0.21	0.86	0.24	89	11 68	0.23	10.72
Mt Biggenden QMMO 16836	1	5 1/8+	1.42	2 42	0.58	0.14	0.96	0.15	77	10.11	0.27	9.07
AMC 140495	3	5+ (4 7/8–5 1/4-)	1.26±0.013 (1.23–1.27)	2.03±0.062 (1.92–2.12)	0.62±0.015 (0.60–0.65)	0.11±0 018 (0.08–0.14)	0.83±0.477 (0.80–0.86)	0.14±0.023 (0.10–0.18)	63.3±5.78 (57–76)	10.77±1.103 (8.83–12.65)	0.23	8.91±0 455 (8 45–9.36)
Mt Goonaneman QMMO 17304	1	5	1.23	1.99	0.62	0.12	0.80	0.15	121	19.32	0.21	9.72
Dan Dan Scrub QMMO 16802	3	5 5/8- (5 1/2–to5 5/8+)	1.50±0.058 (1.40–1.50)	2.38±0.061 (2.26–2.46)	0.63±0.010 (0.62–0.65)	0.12	0.98±0.033 (0.95–1.05)	0.13±0.003 (0.12–0.13)	134.3±7.62 (120–146)	17.91±0.665 (16.89–19.16)	0.25	9.68±0.256 (9.18–10.02)
Colosseum Creek QMMO 13265	3	5 1/8 (4 7/8+to5 3/8)	1.24±0.018 (1.21–1.23)	1.97±0.016 (1.95–1.99)	0.60±0.017 (0.57–0.62)	0.10±0.012 (0.08–0.12)	0.84±0.020 (0.82–0.88)	0.12±0.015 (0.10–0.15)	104.3±2.91 (99–109)	16.20±1.104 (14.07–17.77)	0.19±0.017 (0.16–0.21)	10 85±0.630 (9.72–11.90)

large whorl count, narrow umbilicus, details of internal penial sculpture and position of penial retractor muscle insertion separate *R. annabelli* from its congeners.

TYPE MATERIAL

HOLOTYPE. QMMO17300, Mt Archer, Rockhampton, MEQ, leaf litter. Collected by G. Annabell, 23 Dec 1978. Height of shell 1.23 mm, diameter 1.89 mm. H/D ratio 0.65. D/U ratio 8.36, whorls 6 1/8.

PARATYPES: QMMO8348, 26 specimens, same collection data as holotype: Mt Archer, Rockhampton, MEQ, about one third of the way up (23°21'S, 150°35'E), remnant vine thicket in gully (62, QMMO-11659, QMMO11919, 30 Jun 1982, J. Stanisic); Gavial Creek, Bouldercombe MEQ (23°34'S, 150°28'E), MVF, litter (24, QMMO16807, 9 July 1983, J. Stanisic, D. Potter); Bouldercombe, W of Rockhampton, MEQ, rainforest litter (10, QMMO-12827, 3 Feb 1980, V. Kessner); c. 7 km E of Mt Morgan, MEQ (23°38'S, 150°28'E) MVF/NVF, litter (1, QMMO17301, 11 Jul 1980, J. Stanisic, A. Green; 5, QMMO13117, 29 Jun 1982, J. Stanisic; 4, QMMO-11633, 29 Jun 1982; J. Stanisic); W side of Mt Moore, SW of Gladstone, MEQ, in patch of vine thicket, litter (24°02'S, 151°05'E) (5, AMC137875, QMMO13203, 5 Sept 1982, AM/QM-ABRS).

OTHER MATERIAL

Calliungal, MEQ (1, AMC264, C.T. Musson); W of Gladstone, MEQ, under leaves on ground in bottle tree scrub (1, AMC32996, Aug 1908, S.W. Jackson).

DIAGNOSIS

Shell diameter 1.77–2.36 mm (mean 2.00 mm) with 5 3/8 to 6 1/8 (mean 5 3/4-) tightly coiled whorls, the last descending more rapidly. Apex and early spire (Fig. 140c) flattened to depressed. SP/BWW ratio 0.11–0.26 (mean 0.16), height 1.13–1.54 mm (mean 1.28 mm). H/D ratio 0.52–0.69 (mean 0.63). Protoconch of 1 5/8 to 1 3/4 whorls, mean diameter 343.5 μm at 1 1/2 whorls. Apical sculpture (Fig. 140e) of short segments arranged in 14–18 spiral rows crossing a series of curved, broad radial ribs and ridges. Postnuclear sculpture (Fig. 140f,g) of fine, widely spaced, weakly protractively sinuated radial ribs, 34–51 (mean 41.3) on the body whorl. Ribs/mm 5.60–7.45 (mean 6.62). Microsculpture (Fig. 140f) of very fine radial riblets, 9–16 between each pair of major ribs, crossed by low spiral cords which are raised at their junction with the microradials, producing a beaded effect. Umbilicus (Fig. 140b,h) very narrow, U-shaped to completely closed by reflection of the columellar margin, diameter 0.23–0.27 mm (mean 0.25 mm). D/U ratio 6.85–8.54 (mean 7.66). Sutures impressed. Whorls shouldered above and rounded below a laterally compressed periphery (Fig. 140c). Aperture roundly lunate. Lip simple, columella slightly to strongly reflected over the umbilicus. Parietal callus well developed. Colour golden-yellow horn. Based on 19 measured adults.

Epiphallus (Fig. 141a) muscularised with ascending and descending arms, internally with well developed transverse thickenings (Fig. 141b), entering penis through a simple pore surrounded by a large circular pilaster. Penis (Fig. 141b) elongate, with a short basal extension (Fig. 141a), internally with strong pustules and irregularly shaped pad-like thickenings (Fig. 141b). Penial retractor muscle (Fig. 141a) inserted at the epiphallus - vas deferens junction.

Radula (Fig. 140d) with central tooth slightly smaller than laterals.

Based on 3 dissected specimens (QMMO-11633).

RANGE AND HABITAT

In leaf litter in dry microphyll vine forests and vine thickets between Gladstone and Rockhampton, SEQ.

REMARKS

The shift in insertion of the penial retractor muscle to the epiphallus - vas deferens junction is most likely related to whorl count increase.

Rotacharopa kessneri sp. nov.
(Figs 143–145; Tables 26, 29)

ETYMOLOGY

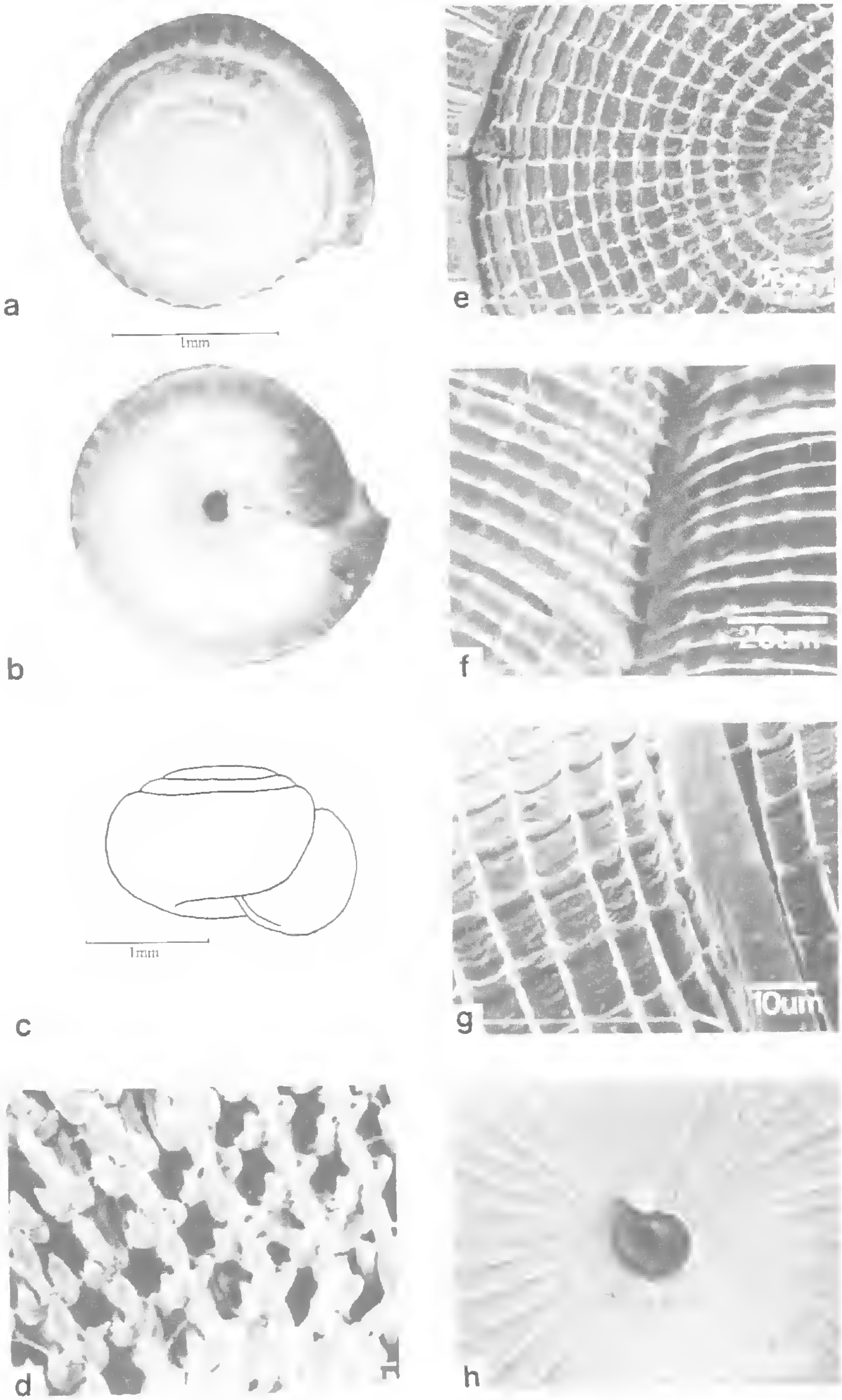
For Vince Kessner, in recognition of his contribution to Australian malacology.

COMPARISONS

R. kessneri differs from *R. densilamellata* in having coarser sculpture, a less elevated spire and narrower umbilicus. Anatomically it lacks the very long penial extension of *R. densilamellata*.

TYPE MATERIAL

HOLOTYPE: QMMO17302, c. 8 km from Kalpowar on Fireclay Rd, Kalpowar S.F., SEQ (24°43'S, 151°21'E), MVF/*Araucaria*, litter. Collected by J. Stanisic, A. Green, 15 Jul 1980. Height of shell 1.40 mm, diameter 2.28 mm, H/D ratio 0.61, D/U ratio 11.12, whorls 5 1/4+.


a
1mm
e
b
f
20um
c
1mm
g
10um
d
h

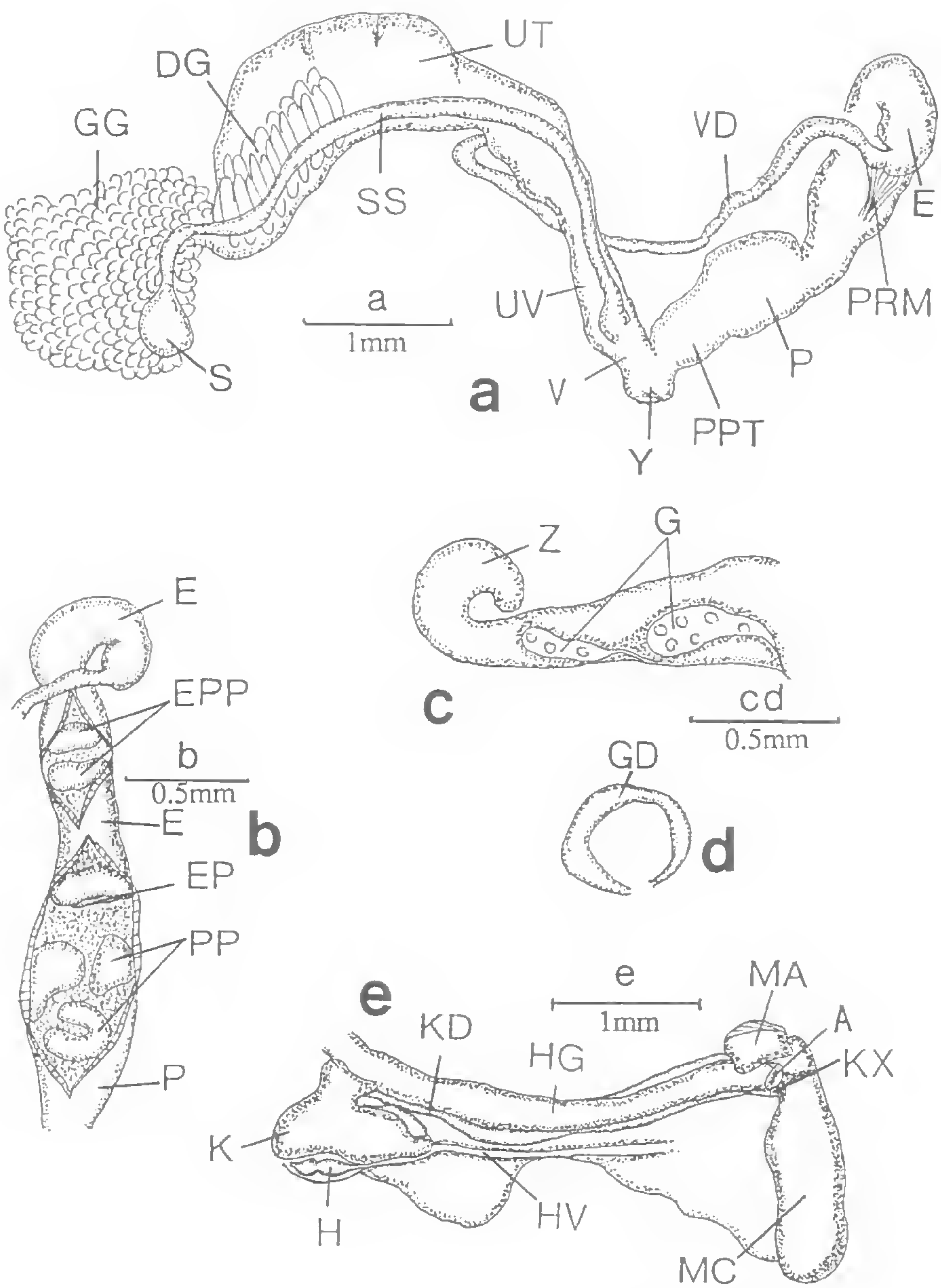


FIG. 141. *Rotacharopa annabelli* sp. nov. c. 7km E of Mt Morgan, SEQ. QMMO11633. a, genitalia; b, details of penis interior; c, ovotestis; d, hermaphroditic duct; e, pallial cavity. Scale line as marked.

FIG. 140. *Rotacharopa annabelli* sp. nov. a–c, Mt Archer, Rockhampton, MEQ. QMMO17300, holotype; d, c. 7km E of Mt Morgan, MEQ. QMMO11633, paratype; e–h, same data as holotype,. QMMO8348, paratype. a–c, entire shell; d, lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, details of microsculpture; h, base. Scale lines as marked.

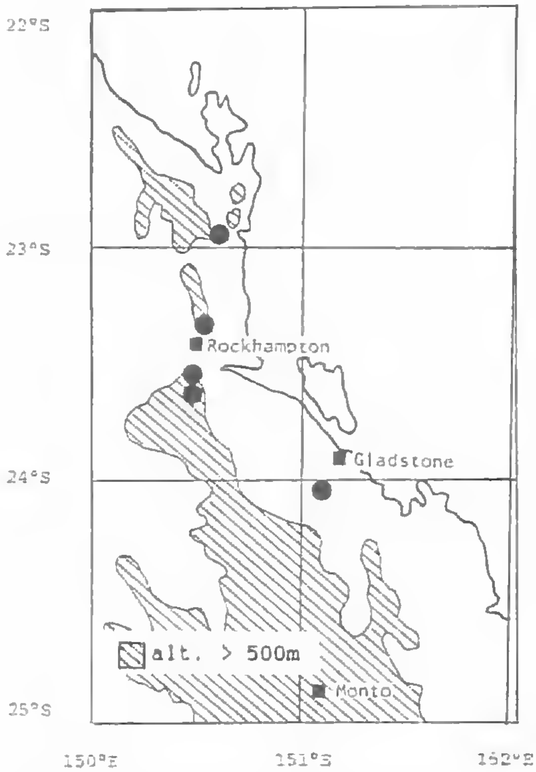


FIG. 142. Distribution of *Rotacharopa annabelli* sp. nov.

PARATYPES: QMMO17303, 6 specimens, same data as holotype; Mt Goonaneman, via Childers, SEQ, rainforest (3, QMMO17304, 7–8 Feb 1981, R. Raven, G. Monteith); high up on river bank beside road, Cania Gorge, SEQ (24°41'S, 150°58'E), rainforest, litter (2, QMMO17305, 14 Jul 1981, J. Stanisic, A. Green); Dan Dan Scrub, SEQ, SEVT, litter (4, QMMO16802, 10 May 1984, J. Stanisic, D. Potter); Mt Biggenden, SEQ, SEVT on limestone outcrop, litter (1, QMMO16836, 3 Jul 1984, J. Stanisic, D. Potter, K. Emberton); SW of Miriam Vale, Qld, Colosseum Ck, rainforest along creek (24°23'S, 151°27'E) (8, AMC137895, QMMO13265, 6 Sept 1982, AM/QM-ABRS); Mt Fort William, Kalpowar S.F., SEQ, NVF (24°39'S, 151°20'E) (3, AMC136758, QMMO12599, 4 Sept 1982, AM/QM-ABRS); W of Childers, Limestone Ck S.F. (25°15'S, 151°55'E) (5, AMC137830, QMMO13127, 3 Sept 1982, AM/QM-ABRS); Rainforest walk, Kalpowar S.F., MVF, SEQ (24°41'S, 151°21'E) (3, AMC136743, QMMO12575, 4 Sept 1982, AM/QM-ABRS).

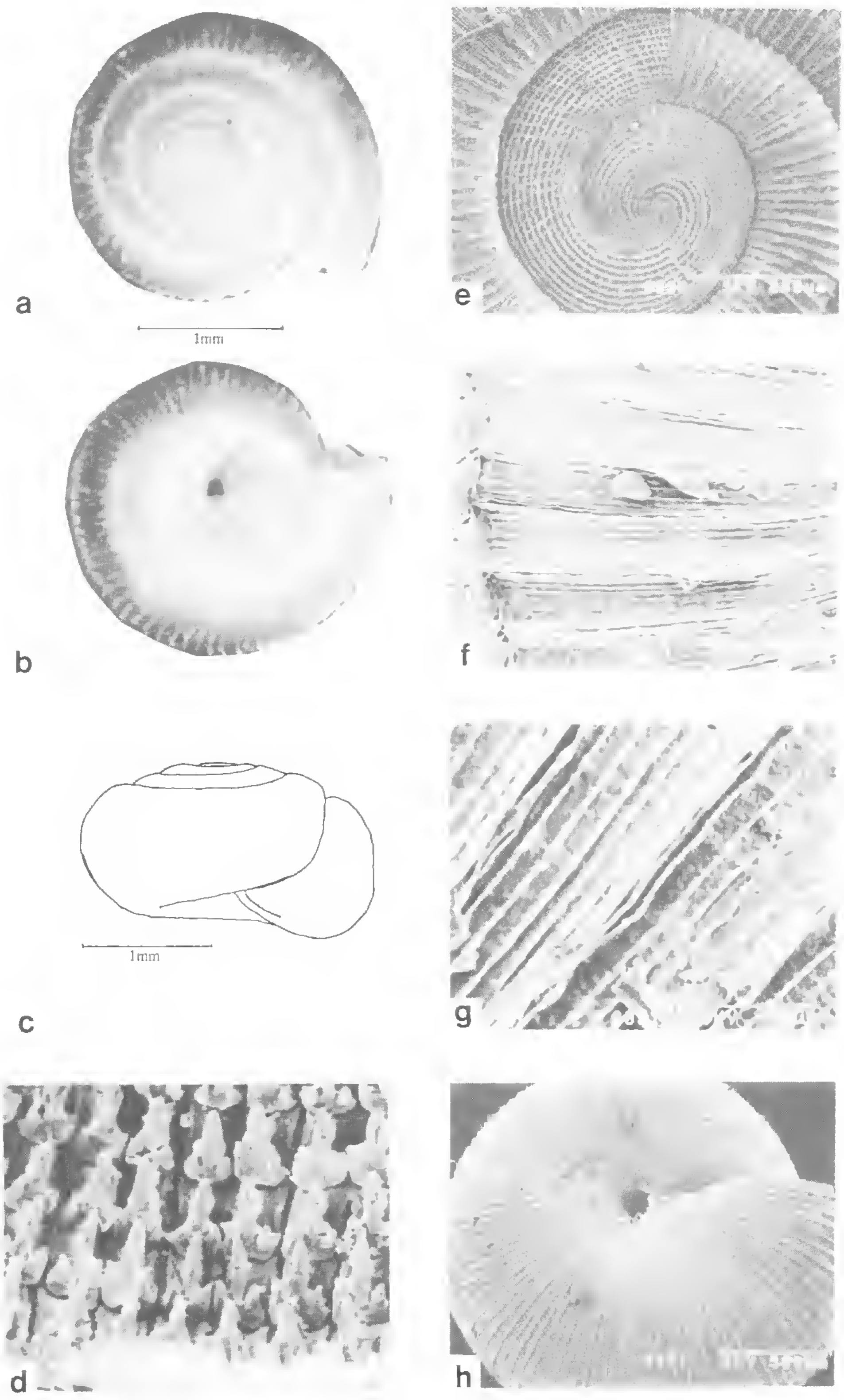
OTHER MATERIAL

Bulburin S.F., S of Gladstone, SEQ, 580 m (24°34'S, 151°29'E) (1, AMC152210, 8 May 1975, J.B. Burch, W.F. Ponder, P.H. Colman); Bulburin S.F., S of Gladstone, SEQ, 540 m, CNVF-A1 forest type (24°31'S, 151°29'E) (11, AMC152211, 8 May 1975, W.F. Ponder, J.B. Burch, P.H. Colman); Bobby Range S.F., SEQ, NVF (24°37'S, 151°32'E) (12, AMC136504, QMMO12138, 6 Sept 1982, AM/QM-ABRS); Clifton Range S.F., SW of Fairlies Knob N.P., SEQ, Vine thicket/*Araucaria* (25°34'S, 152°16'E) (2, AMC136672, QMMO12376, 2 Oct 1982, AM/QM-ABRS); c. 12.1 km NW Granite Creek Crossing, on Bobby Range - Mt Perry Rd, SEQ, NVF/palms, under logs (2, QMMO16844, 16 Sept 1985, J. Stanisic, D. Potter); summit, Mt Booroon Booroon, SW of Miriam Vale, SEQ, MVF/*Araucaria*, among rocks (5, QMMO16849, 17 Sept 1985, J. Stanisic, D. Potter).

DIAGNOSIS

Shell diameter 1.85–2.46 mm (mean 2.15 mm) with 4 7/8- to 5 5/8+ (mean 5+) tightly coiled whorls, last whorl descending more rapidly. Apex flat (Fig. 143c), spire slightly to moderately elevated. SP/BWW ratio 0.10–0.24 (mean 0.15), height 1.15–1.60 mm (mean 1.31 mm), H/D ratio 0.57–0.65 (mean 0.61). Protoconch of 1 5/8 whorls, mean diameter 385.7 μm at 1 1/2 whorls. Apical sculpture (Fig. 143e) of short segments arranged in spiral rows and curved, broad radial ridges and ribs. Postnuclear sculpture (Fig. 143f,g) of fine, moderately spaced to crowded, weakly protractively sinuated radial ribs, 57–146 (mean 95.8) ribs on the body whorl. Ribs/mm 8.83–19.32 (mean 14.19). Microsculpture (Fig. 143f) of fine radial riblets, 5–10 between each pair of major ribs, and low spiral cords which are raised at their junction with the microradials to form a bead. Umbilicus (Fig. 143b,h) narrow, U-shaped, diameter 0.16–0.29 mm (mean 0.23 mm). D/U ratio 7.23–11.90 (mean 9.71). Sutures impressed, whorls shouldered above and rounded below a broadly rounded periphery (Fig. 143c). Aperture broad, roundly lunate. Lip simple, columella margin slightly twisted toward umbilicus. Parietal cal-

FIG. 143. *Rotacharopa kessneri* sp. nov., a–c, c. 8km from Kalpowar on Fireclay Rd, Kalpowar S.F., SEQ, QMMO17302, holotype; c. 12.1km N of Granite Ck crossing, Bobby Range, SEQ, QMMO16844; e–h, Colosseum Ck, SW of Miriam Vale, SEQ, QMMO13265, paratype. a–c, entire shell; d, central and lateral teeth; e, apical sculpture; f, post nuclear sculpture; g, details of microsculpture; h, base. Scale lines as marked.


a
1mm
b
c
1mm
d
e
f
g
h

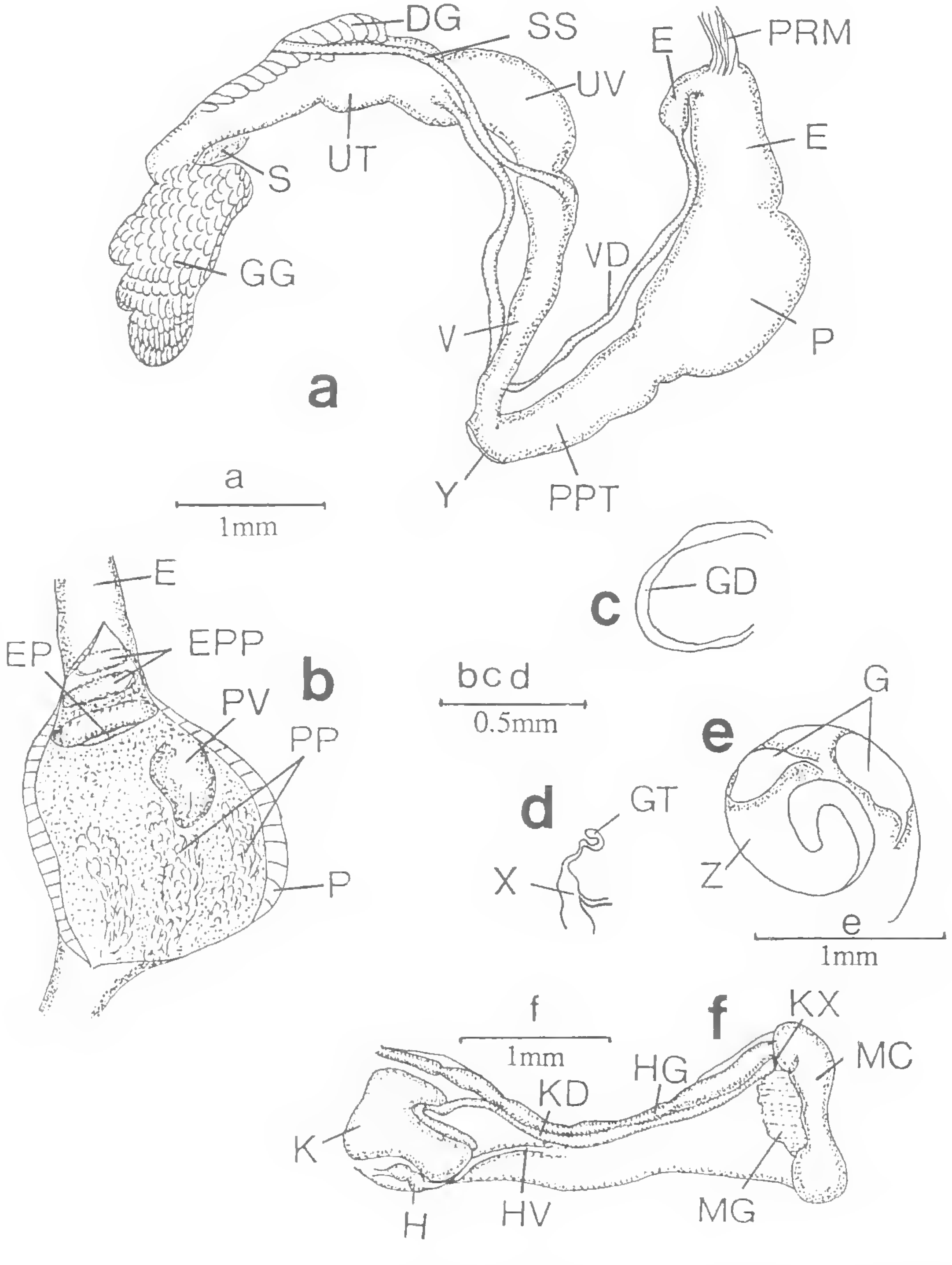


FIG. 144. *Rotacharopa kessneri* sp. nov. Summit, Mt Booroon Booroon, SW of Miriam Vale, SEQ. QMMO16849. a, genitalia; b, details of penis interior; c, hermaphroditic duct; d, talon and carrefour; e, ovotestis; f, pallial cavity. Scale lines as marked.

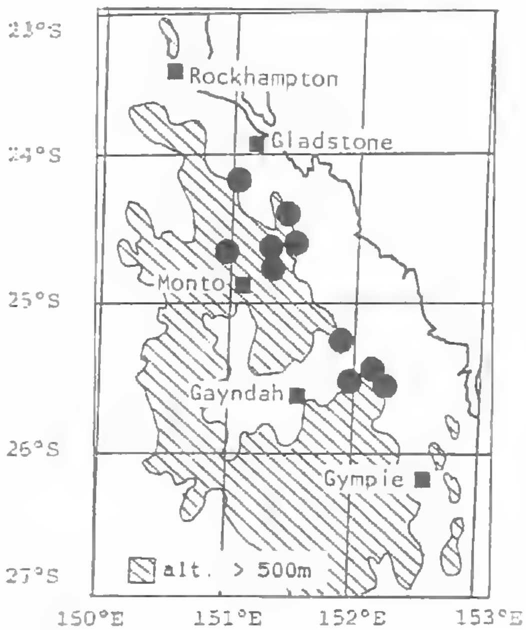


FIG. 145. Distribution of *Rotacharopa kessneri* sp. nov.

lus developed. Colour beige to light-golden horn. Based on 18 measured adults.

Epiphallus (Fig. 144a) with short, narrow ascending arm and much wider descending arm that has thick, transverse, fleshy pilasters internally (Fig. 144b). Epiphallic pore (Fig. 144b) simple, surrounded by a weak fleshy collar. Penis (Fig. 144a) with a wide upper chamber, a lower, cylindrical section, and a basal extension (Fig. 144a). Internally, penis with strong pustulations arranged into longitudinal thickenings (Fig. 144b) and an apical conical verge. Penial retractor muscle (Fig. 144a) inserting on the epiphallus at the point of reflexion.

Radula (Fig. 143d) typical.

Based on 4 dissected specimens (QMMO-16849, QMMO16844).

RANGE AND HABITAT

Under logs in dry microphyll vine forests and vine thickets between Biggenden and Calliope, SEQ. It has also been found in the wetter warm subtropical notophyll vine forests of the Bobby Range and Mt Fort William. The species appears to be able to tolerate drier conditions and occurs in 'fringe' rainforest in the Cania Gorge, near Monto, SEQ.

REMARKS

R. kessneri may be sympatric with *R. annabelli* because the two species have been collected within only a few kilometres of each other west of Gladstone, SEQ.

Rotacharopa densilamellata sp. nov.
(Figs 146–148; Tables 26, 30)

ETYMOLOGY

Latin *densus*, crowded; and *lamella*, plate; referring to the postnuclear sculpture of crowded ribs.

COMPARISONS

The small, globose shell with many tightly coiled whorls, elevated spire, crowded, fine radial ribs, and small umbilicus, identify *R. densilamellata* in SEQ. Anatomically the peculiar preputial extension of the penis (Fig. 147a) is distinctive. The only other species apt to be confused with *R. densilamellata* is the sympatric *Egilomen globosa*, but it has adult sculpture of fewer, broad radial ribs, a completely closed umbilicus, and a sinuate lip with apertural sinus.

TYPE MATERIAL

HOLOTYPE: QMMO17296, Kenilworth S.F., SEQ (26°37'S, 152°42'E) rainforest, leaf litter. Collected by J. Stanisic, A. Green. Height of shell 1.38 mm, diameter 1.95 mm, H/D ratio 0.71, D/U ratio 5.27, whorls 4 3/4-.

PARATYPES: QMMO17297, 4 specimens, same collection data as holotype; sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ (27°04'S, 152°41'E) NVF/Araucaria (20, QMMO15081, 6 Sept 1983, J. Stanisic, D. Potter); Kenilworth S.F., SEQ (26°35'S, 152°36'E) mixed NVF (12, QMMO6285, 18 May 1976, M.J. Bishop); Fred's Rd, Mt Mee, SEQ (27°05'S, 152°43'E) rainforest, leaf litter (11, QMMO8347, 14 Apr 1980, J. Stanisic, N. Hall, A. Green; (6, QMMO15984, 28 Oct 1984, J. Stanisic, G. Annabell); Little Yabba Creek, Imbil S.F., SEQ (26°28'S, 152°38'E) NVF (4, QMMO12018, AMC-136435, 8 Sept 1982, AM/QM-ABRS); Kenilworth S.F., SEQ (26°40'S, 152°36'E) *Araucaria*, leaf litter (12, QMMO8346, 22 May 1980, J. Stanisic, A. Green); c. 25.5 km and 28.5 km from Goomburra on Goomburra S.F. Road, SEQ NVF/Palms/*Araucaria* (8, QMMO12694, AMC136815, 7 Dec 1981, AM/QM-ABRS; 1, QMMO11125, 16 Mar 1981, AM/QM-ABRS); 'Rainforest Park', near Maleny, on Maleny-Montville Rd, SEQ NVF, under log (1, QMMO11883, 5 Dec 1982, J. Stanisic); Kenilworth S.F., SEQ (26°35'S, 152°42'E) c. 80 m, rainforest/eucalypt

TABLE 90. LOCAL VARIATION IN *ROTACHAROPA DENSILAMELLATA* SP. NOV. (MEAN, SEM AND RANGE)

NAME	NUMBER OF SPECIMENS	WHORLS	HEIGHT (mm)	DIAMETER (mm)	H/D RATIO	SPIRE PROTRUSION (mm)	BODY WHORL WIDTH (mm)	SP/BWW RATIO	RIBS	RIBS/MM	UMBILICAL WIDTH (mm)	D/U RATIO
Rotacharopa densilamellata												
Kenilworth QMMO17296 (Holotype)	1	4 3/4	1.38	1.95	0.71	0.23	0.82	0.28	125	20.37	0.37	5.27
Kenilworth QMMO8346	2	4 3/4 (4 5/8+ to 4 7/8+)	1.30±0.065 (1.23–1.36)	1.82±0.010 (1.81–1.83)	0.71±0.030 (0.68–0.74)	0.22±0.030 (0.19–0.25)	0.75±0.030 (0.72–0.78)	0.30±0.030 (0.26–0.32)	93	16.18	0.36±0.010 (0.35–0.37)	5.06±0.120 (4.94–5.18)
Kenilworth QMMO6284	2	4 7/8 (4 3/4–5)	1.31	1.89±0.020 (1.87–1.91)	0.70±0.005 (0.69–0.70)	0.20±0.035 (0.16–0.23)	0.77±0.010 (0.76–0.78)	0.26±0.045 (0.21–0.30)	121.5±7.50 (114–129)	20.44±1.04 (19.40–21.48)	0.37	5.05
Mt Mee QMMO15081	2	5 5/8+ (5 5/8–5 3/4)	1.52	2.09	0.73	0.34±0.030 (0.31–0.37)	0.80	0.42±0.040 (0.38–0.46)	143	21.72	0.49±0.020 (0.47–0.51)	4.26±0.180 (4.08–4.44)
QMMO12176	2	5 5/8 (5 3/8+ to 5 7/8–)	1.31±0.075 (1.23–1.38)	2.05	0.62	0.31±0.060 (0.25–0.37)	0.85±0.050 (0.80–0.90)	0.36±0.050 (0.31–0.41)	132		0.43±0.040 (0.39–0.47)	5.26
QMMO8347	2	5 1/8 (5 1/4–5 1/2)	1.29±0.055 (1.23–1.34)	1.65	0.72	0.28±0.030 (0.25–0.31)	0.79±0.030 (0.76–0.82)	0.35±0.030 (0.32–0.38)	124	21.34	0.47	
Montville QMMO11980	1	5 1/4	1.40	1.79	0.78	0.39	0.74	0.53	206	36.68	0.35	5.12
Maleny QMMO11883	1	4 7/8	1.23	1.85	0.67	0.21	0.74	0.28	133	22.89	0.37	4.99
Cunninghams Gap QMMO12676	1	5	1.50	2.16	0.70	0.27	0.82	0.33	128	18.88	...	...

emergents (22, QMMO6284, 3 May 1976, M.J. Bishop); Cunninghams Gap N.P., SEQ, near monument, 755 m, SNVF/ferns (28°04'S, 152°24'E) (104, AMC136805, QMMO12676, 7 Dec 1981, AM/QM-ABRS); Montville Rd near Kondalilla Falls N.P., SEQ, vine scrub on roadside (26°40'S, 152°52'E) (2, AMC136411, QMMO11980, 8 Sept 1982, AM/QM-ABRS); Cunninghams Gap N.P., SEQ, near monument, MVF/*Araucaria* (28°04'S, 152°24'E) (10, AMC128609, QMMO10993, 16 Mar 1981, AM/QM-ABRS); sidetrack off Mt Archer Rd, Mt Mee S.F., SEQ NVF/*Araucaria* (27°04'S, 152°41'E) (6, QMMO12176, AMC136522, QMMO12179, 31 Sept 1982, AM/QM-ABRS).

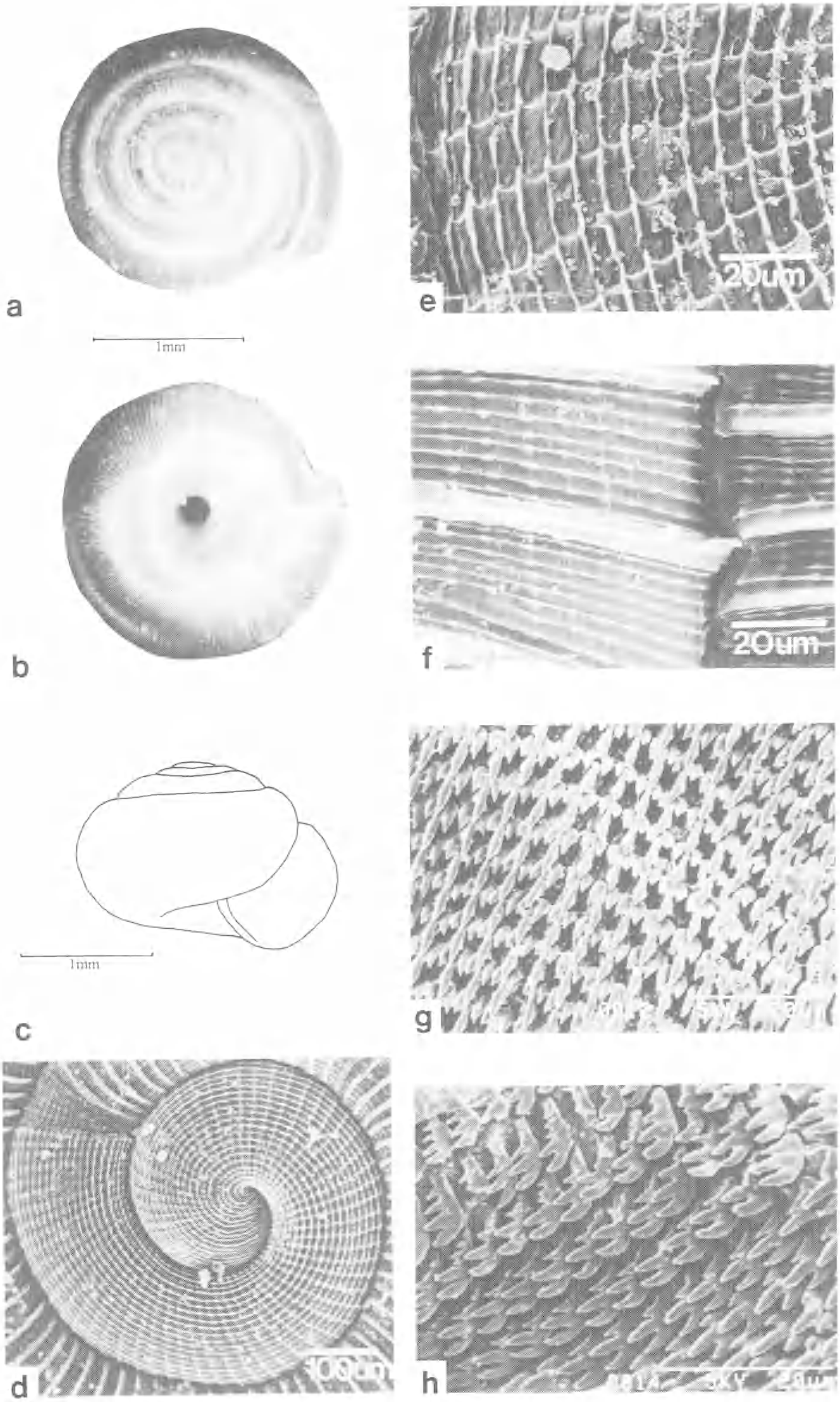
Other Material

Little Yabba S.F., SEQ (26°34'S, 152°39'E) c. 160 m, eucalypt and vine forest (1, QMMO6301, 3 May 1976, M.J. Bishop); Maiala N.P., Mt Glorious, SEQ, NVF, leaf litter (1, QMMO11853, 20 Jun 1982, MSA party); Boombana N.P., Mt Nebo, SEQ, wet sclerophyll (1, QMMO6298, Aug 1976, M.J. Bishop); Campbell's Camp, Kenilworth S.F., SEQ (26°42'S, 152°37'E) CNVF, leaf litter (1, QMMO17298, 1 Jul 1980, J. Stanisic, A. Green); Cunningham's Gap, SEQ, leaf litter (1, QMMO17299, 18 Jun 1979, G. Annabell); c. 0.3 km N of Little Yabba Ck. on Maleny-Kenilworth Rd, Kenilworth S.F., SEQ (26°37'S, 152°42'E) litter (2, QMMO13434, 19 May 1983, K. Collins, J. Stanisic).

Diagnosis

Shell diameter 1.79–2.16 mm (mean 1.94 mm) with 4 5/8+ to 5 7/8- (mean 5 1/8+) tightly coiled whorls, last whorl descending slowly. Spire elevated (Fig. 146c), apex tending to be flattened, SP/BWW ratio 0.21–0.53 (mean 0.34), height 1.23–1.52 mm (mean 1.35 mm). H/D ratio 0.67–0.78 (mean 0.71). Protoconch of 1 1/2 to 1 5/8 whorls, mean diameter 428.3 μm at 1 1/2 whorls. Apical sculpture (Fig. 146d,e) of short segments arranged in 19–25 prominent crowded spiral rows overlying broad, curved radial ribs and ridges. Postnuclear sculpture (Fig. 146f) of narrow, crowded, weakly protractively sinuated radial ribs, 93–206 (mean 139) on the body whorl, whose interstices are 4–5 times their width. Ribs/mm 16.18–36.68 (mean

FIG. 146. *Rotacharopa densilamellata* sp. nov. a-c, Kenilworth S.F., SEQ. QMMO17296, holotype; d-f, same data as holotype. QMMO8346, paratype; g-h, Cunningham's Gap, SEQ. QMMO12676, paratype. a-c, entire shell; d, apical sculpture; e, details of apical spiral cords; f, post nuclear sculpture; g, central and lateral teeth; h, marginal teeth. Scale lines as marked.


a
e
20um
1mm
b
f
20um
1mm
c
g
d
h

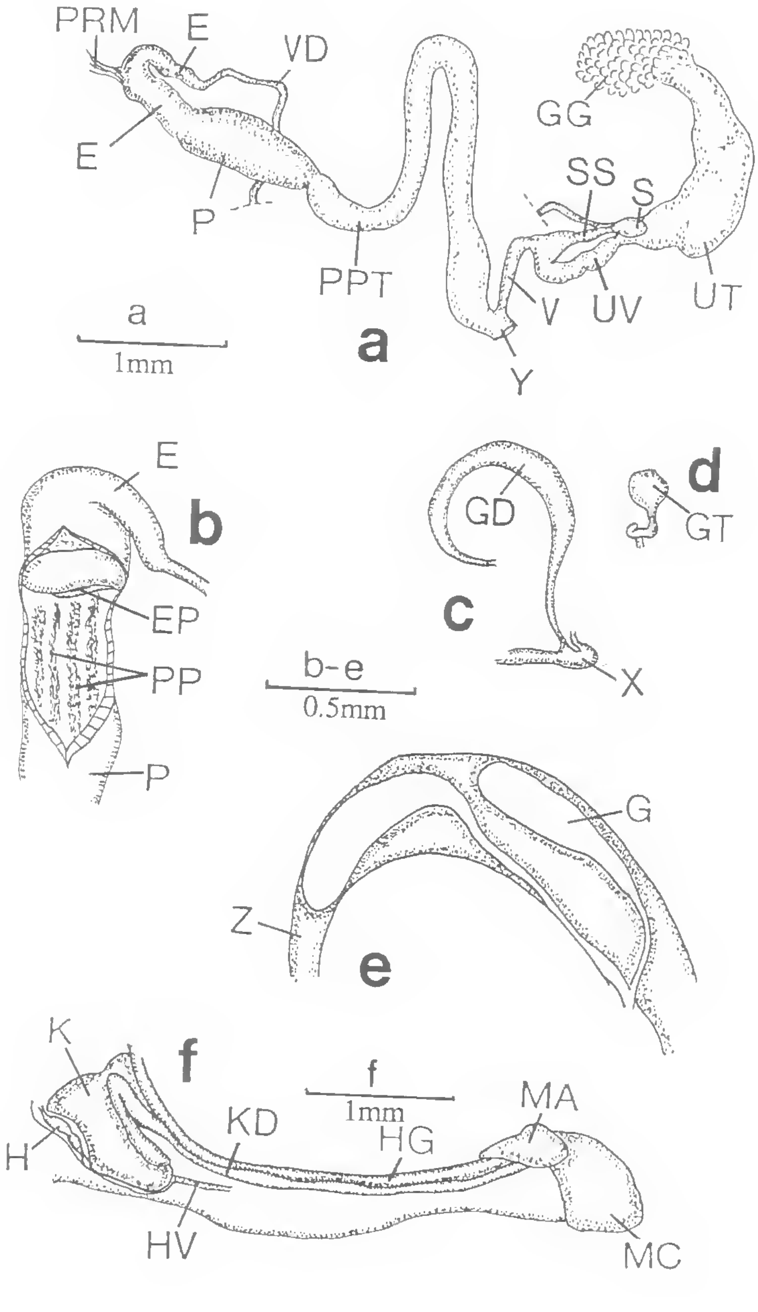


FIG. 147. *Rotacharopa densilamellata* sp. nov. Cunningham's Gap N.P., SEQ. QMMO10993, QMMO12676, paratypes. a, genitalia; b, details of penis interior; c, hermaphroditic duct and carrefour; d, talon; e, ovotestis; f, pallial cavity. Scale lines as marked.

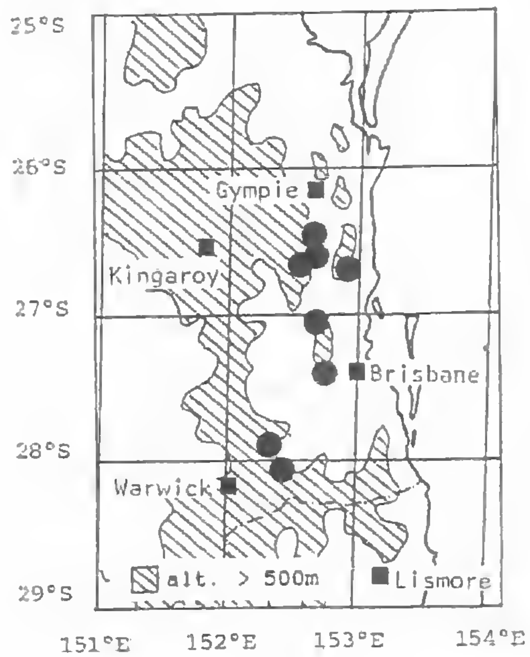


FIG. 148. Distribution of *Rotacharopa densilamellata* sp. nov.

22.10). Microsculpture (Fig. 146f) of very fine radial riblets, 6–10 between each pair of major ribs, and equally fine spiral cords, which are raised at their intersection with the microradials producing a beaded effect. Umbilicus (Fig. 146d) narrow, U-shaped, diameter 0.35–0.51 mm (mean 0.41 mm). D/U ratio 4.08–5.27 (mean 4.93). Sutures impressed. Whorls shouldered above and rounded below the periphery (Fig. 146c). Aperture roundly lunate. Lip simple, columella slightly deflected toward umbilicus. Parietal callus strongly developed. Colour light-brown. Based on 14 measured adults.

Epiphallus internally with transverse pilasters, entering penis apically through a simple pore (Fig. 147b). Penial retractor muscle (Fig. 147a) inserted on epiphallus at the point of reflexion. Penis (Fig. 147b) thin walled, with a very long preputial extension (Fig. 147a), internally with a simple, apical epiphallic entrance, and strongly pustulose walls; pustules arranged in vague longitudinal rows (Fig. 147b).

Radula (Fig. 146g,h) typical.

Based on 4 dissected specimens (QMMO10993, QMMO12676).

RANGE AND HABITAT

Disjunct distribution in cool subtropical notophyll vine forests of the Great Dividing Range in southern Queensland, and the warmer subtropical notophyll vine forests of the D'Aguilar, Conondale and Blackall Ranges, SEQ. It lives under logs.

REMARKS

R. densilamellata has a more elevated spire than either of its congeners and the longer preputial tube may be a secondary modification related to this height increase.

There appears to be considerable interpopulational variation in the shells of *R. densilamellata* but much of the available material is subadult and not suitable for statistical analysis.

EXTRALIMITAL RELATIONSHIPS

Attempts to relate the Charopidae reviewed in this study to extralimital charopids remain tentative because of the lack of knowledge about some of the major regional charopid faunas.

Solem (1983) reviewed the Pacific Basin species but only briefly mentioned the large radiations of New Caledonia, Lord Howe Island and Norfolk Island. Climo (1969, 1970, 1971, 1978, 1980, 1981, 1983) reviewed a large number of New Zealand species, but omitted important comparative data on shell sculpture and anatomy. Additionally, a large number of New Zealand charopids are still undescribed (Solem, Climo and Roscoe, 1981, p. 454). Locally, the Australian charopid fauna has thus far received scant attention with only Solem (1984), Smith and Kershaw (1985) and more recently Stanisic (1987) presenting significant detail on a handful of species. Nevertheless broad comparative observations are possible.

SHELL PATTERNS

The extent of conchological variation in Australian species is similar to that in New Zealand charopids but contrasts with the relative stability shown by Pacific Basin taxa.

With the exception of *Microcharopa mimula* Solem, 1983 and the widespread *Discocharopa aperta* (Möllendorff, 1888), apical sculpture in Pacific Island species consists of spiral cords. Patterns of apical sculpture in New Zealand species may be spiral, radial, reticulate, smooth or otherwise modified (Climo, 1969b, 1970, 1981, 1983). Among species examined in this study, a combination of curved radial ribs and weaker spiral cords is common. Spiral apical sculpture, dominant among Pacific Island species, is present only in *Setomedea*, *Omphaloropa varicosa* and the extralimitally related *Sinployea intensa*.

The pitted apical sculpture of *Biomphalopa*, *Nautiliropa omicron* and *Gyrocochlea curtisiana* (Figs 60c, 63d, 54e, 57c) has not been reported for Pacific Island or New Zealand Charopidae but is seen in the primarily Papua New Guinean *Pilsbrycharopa*. Solem (1984) recorded this sculptural feature for *Pilsbrycharopa tumidus* (Odhner, 1917) from the Northern Territory, Australia. These taxa may be distantly related but considering that this sculpture is derived from the more common reticulate pattern (see discussion for *Gyrocochlea curtisiana*), it is likely to have developed independently in the New Guinean genus. The pitted apical sculpture seen in *Ngairea murphyi*, *Letomola contortus*, *Lenwebbia protoscrobiculata* and *Hedleyoconcha* (Figs 9f, 23e, 26d, 29g, 67d) is grossly similar to that of the New Zealand *Paracharopa* Climo, 1983. In these cases however, the macroscopic similarity has quite different underlying microstructure which correlates with major anatomical differences.

Apical sculpture of *Rotacharopa* is identical to that in the Pacific Basin *Microcharopa mimula* Solem, 1983 and North American *Radiodiscus millecostatus* Pilsbry and Ferriss, 1906 although whorl numbers and coiling pattern indicate important regional differences in these rotadiscines.

The postnuclear sculptures of Australian, New Zealand and Pacific Island species share similarities which are probably convergent and related to sharing a common niche. However, in contrast with the conservatism of Pacific Basin species, the Australian charopids display the same rich range of variation seen in the New Zealand fauna. Sculptural reduction, common among New Zealand and Australian species, is rare in Pacific Island charopids. Comparison of rib counts of Australian (Table 1) and Pacific Island species (Solem, 1983, Table 1) shows that the median rib count in the latter is greater. It is premature to say whether this will prove to be a basic difference between these two charopid faunas.

The most unusual postnuclear sculptural elements among Australian subtropical Charopidae are the incised spiral lines of *Ngairea*, *Lenwebbia* and to lesser extent *Mussonula*. This feature, which is more typical of helicarionids, is confined to the group of genera with incomplete secondary ureters. No equivalent condition has been reported in any extralimital charopids.

Shell shape of Australian and New Zealand species is more diverse than that of Pacific Island species which, with a single exception, are a monophyletic assemblage spread over a number of islands (Solem, 1983). It appears that the Australian and New Zealand charopids have had a more complex evolutionary history involving many radiations and extinctions under conditions of high intra-site diversity where competition for food and space has led to considerable variation in shell form. Consequently shell elevation and associated umbilical closure is a more frequent occurrence in Australian and New Zealand charopids than in Pacific Island species. Accordingly, Solem and Climo (1985) showed that development of a keel, periostracal processes and shell colour in New Zealand species are site-preference correlated and not based on monophyletic assemblages. These authors also found that in the development of large sympatric snail communities evolution appears to favour an increase in diversity of shell shape. In such situations convergences will occur and are highlighted in the Australian-New Zealand species pairs of *Hedleyoconcha delta* - *Serpho kivi* (Gray, 1853) and *Setomedea seticostata* - *Suteria ide* (Gray, 1850).

Barrier formation is extensive among Pacific Island and New Zealand Charopidae but occurs to a lesser extent in Australian subtropical taxa. Solem (1973; 1983, p. 15) discussed the polyphyletic origin of barriers in Pacific Basin species and Climo (1978) provided evidence for polyphyletic origin in New Zealand species. The form, number and microsculpture (Figs 78e, 81d) of the barriers in *Rhophodon* make them comparable to the barriers in Pacific Island taxa such as *Semperdon* Solem, 1983, and New Zealand *Ptychodon* Ancey, 1888. However the reduced structures of *Letomola contortus* (Fig. 68a,b) are less easily related to Pacific taxa, being grossly similar to the barriers seen in New Zealand *Fectola* Iredale, 1915 (Climo, 1978).

Anatomical Patterns

Pallial configurations of species reviewed are most similar to those of New Zealand Charopidae. All endemic Pacific Island species possess a kidney in which the lobes are subequal, equal or the rectal lobe is much longer than the pericardial lobe (Solem, 1983). In contrast New Zealand species for which data is available (Climo, 1980, 1983; Solem, 1983), have pericardial longer than rectal lobe. *Letomola contortus*, *Egilomen cochlidium*, *E. globosa* and *Sinployea intensa* have equal to subequal kidney lobes (Figs 69g, 129d, 132f, 138f) while the remainder have the pericardial lobe much longer than the rectal lobe.

An incomplete secondary ureter was previously recorded in the Charopinae only in *Oreokera cumulus* (Odhner, 1917) and *O. nimbus* Stanisic, 1987 from north Queensland, and *Amphidoxa marmorella* (Pfeiffer, 1850) from Juan Fernandez. This is a primitive condition in the Charopidae (Solem, 1983; Stanisic 1987). Its presence in genera such as *Hedleyoconcha*, *Setomedea* and *Ngairea*, which all show typically disjunct relict distributions, is not surprising, and a similar condition in southern Australian and New Zealand species would not be unexpected. Shortened secondary ureters have been reported for some extralimital Rotadiscinae (Baker, 1927) but were not present in rotadiscine species reviewed here.

Intrusive mantle-gland tissue was noted in the majority of species examined. This structure is rare in Pacific Island species and present only in *Graeffdon graeffei* (Mousson, 1869) and *Semperdon xyleborus* (Solem, 1983). Extent of its occurrence in New Zealand species is not known but it has been recorded for *Charopa coma* (Gray, 1843) and *Phenacohelix pilula* (Reeve, 1852).

In local species the ovotestis usually consists of two clumps of palmately clavate to finger-like lobes of alveoli oriented parallel to the plane of coiling and embedded in the apical whorls of the digestive gland. Occasionally lobes assume a right angle orientation and may vary in size and number. All Pacific Island species have ovotestis lobes parallel to the plane of coiling. Information on New Zealand species is scarce although both parallel and right angle orientation have been reported. Stanisic (1987) considered that a right angle orientation of the ovotestis was a primitive character. However, from this study it appears that ovotestis orientation is related to shell height. *Hedleyoconcha*, *Ngairea* and *Lenwebbia* have elevated shells and right-angle orientation of the ovotestis. In contrast, *Setomedea*, which possesses a primitive pallial configuration, has a less elevated shell and the typical parallel orientation. *Gyrocochlea vinitincta* has a biconcave shell, with secondarily enlarged body whorls, and has the ovotestis oriented at right angles.

Number and size of clumps are variable and probably related to variability in whorl count and shell size. *Ngairea murphyi* and *Hedleyoconcha delta* have high whorl counts and multiple clumps of ovotestis (Figs 10d, 24e) while the small *Sinployea intensa* and *Letomola contortus* have single bilobed clumps (Figs 69c, 138e). Among Pacific Island and New Zealand species the 'two clump' condition is typical. Some Pacific Island *Semperdon* Solem, 1983 and *Sinployea* Solem, 1983 show reduction to a single clump but there are no examples of the increase in clumps recorded in some Australian and New Zealand species.

The penis of Pacific Island species is pear-shaped with the penial retractor muscle inserting on the penis head, or epiphallus, very near to the epiphallus-penis junction. The penis lacks a sheath, and internally, has a basic pattern of apical verge, circular ridges and a pocket stimulator. Among Australian subtropical taxa verges are rarely present, penial collars are confined to a handful of genera and a true pocket stimulator is seen only in *Nautiliropa omicron* (Fig. 65c). Instead there is a simple, apical (occasionally subapical) entrance of the epiphallus and few to many longitudinal pilasters which may be modified under conditions of sympatry.

The penes of *Hedleyoconcha* and *Ngairea* have an apical muscular collar (Figs 4b, 10b, 13b, 16b, 24c, 27b) which is comparable with that of the New Zealand *Phenacohelix pilula* (Reeve, 1852) (Solem, 1983, p. 28). Additionally the large fleshy penial pilasters of *Cralopa* are similar to those of the New Zealand *Cavellia sterkiana* (Suter, 1891) and *C. colensoi* (Suter, 1891) (Climo, 1969b).

According to Climo (1980, 1983) *Pulchridomus*, *Aeschrodomus*, *Charopa* and *Phenacocharopa* have a constricting 'sphincter' dividing the penis into distinctly sculptured upper and lower chambers. A similar pattern is seen in *Elsothera sericatula* and *E. genithecata* (Figs 105e, 109b).

Most Australian, New Zealand and Pacific Island species have a well defined epiphallus. However, some New Zealand species lack an externally differentiated epiphallus. A comparable Australian species is *Setomedea janae* in which the epiphallus is partially incorporated into the penial complex (Fig. 39c).

RADULA

The typical charopid radula has tricuspid central and lateral teeth (usually the central tooth is slightly smaller) with long lanceolate mesocone and short pointed ectocones. The marginal teeth are multicuspid and in many instances a transitional zone of lateromarginal teeth is present. This pattern is the rule in Pacific Island and most Australian subtropical species. Notable local exceptions are *Egilomen globosa*, *E. cochlidium* (Figs 128h, 131h), *Omphaloropa varicosa* and *Letomola contortus* (Figs 134h, 68e) which have reduced central teeth. This latter condition is common in New Zealand species (Climo, 1969b, 1970).

The broadly triangular mesocone and bicuspid laterals of *Ngairea* (Figs 3f, 9d, 12d, 15d) are similar to those of the New Zealand *Phenacohelix* (Cumber, 1961). Significantly both are arboreal to semi-arboreal. However, presence of anterior flares on teeth in groups such as *Ngairea* and *Hedleyoconcha* has no known correlative in either New Zealand or Pacific Island taxa.

Nautiliropa omicron has slender hook-like teeth and V-shaped row arrangement (Figs 63e,f). This is a major departure from other subtropical species and also has no equivalent among Pacific Island or New Zealand Charopidae. *N. omicron* is sympatric with the conchologically convergent *Gyrocochlea* and the unusual radula may be a local feature related to intergeneric sympatry.

In summary, Australian subtropical Charopidae display a number of conchological and anatomical features which suggest relationships with New Zealand charopids but also indicate evolution in isolation for some considerable period. At the same time development under similar environmental conditions has led to many convergences in shell features among species of these two regional charopid faunas. Analysis of southern Australian species will be critical in understanding the full extent of possible relationships.

PHYLOGENY

The fifty species of Charopidae reviewed display a wide variety of anatomical and conchological patterns, yet they represent only a small subset of an extensive Australian charopid fauna. The prolific Tasmanian and Victorian faunas, extensive radiations in mideast and northeast Queensland, and a further 60–70 poorly known or undescribed subtropical species are still to be reviewed. Hence the following discussion is preliminary.

Ngairea, *Hedleyoconcha*, *Mussonula*, *Lenwebbia* and *Setomedea* have incomplete secondary ureters and possess a number of conchological specialisations (incised spiral lines, broad spiral grooves, periostracal setae, punctate apical sculpture) which isolate them from the genera with the more typical charopid pallial configuration in which the secondary ureter is complete. They probably had a common ancestor. Their penes have a typical internal pattern of apical collar and longitudinal pilasters. This is well illustrated in *Ngairea* and *Hedleyoconcha*. Together with *Mussonula* and *Lenwebbia* these genera are further characterised by elevated shells with very narrow umbilici. An exception is *N. murphyi* which has secondarily narrowed whorls and a slightly more open umbilicus. *Lenwebbia* can be derived from *Ngairea* through modification of shell sculpture, penis and kidney, and shares the unusual feature of incised spiral lines with *Ngairea* and *Mussonula*.

Setomedea appears to represent an attempt at habitat specialisation among the taxa with incomplete secondary ureters. The relatively small size, peculiar coiling of the primary ureter, and interspecific variability in whorl numbers and shell coiling pattern, are inconsistent with other genera in this group. Unlike *Ngairea* and *Hedleyoconcha* (and probably *Mussonula*), *Setomedea* is not arboreal or semi-arboreal. It usually lives in moist rotting logs and the periostracal setae are probably an adaptation for preventing dirt accumulation on the shell in this comparatively wet microhabitat.

Among the more generalised radially-ribbed groups, *Cralopa* and *Elsothera* stand apart in having altered penial and epiphallic complexes, closed umbilici and conspicuous apertural sinuses. This latter feature is relatively rare in Australian charopids and suggests a possible relationship with New Zealand particularly through *Cavellia* Iredale, 1915. *Cralopa* and *Elsothera* are probably more closely related to each other than to other groups reviewed here.

In spite of size differences, *Biomphalopa* and *Gyrocochlea* show structural consistencies in shell and anatomy which suggest common ancestry. *Gyrocochlea* is an evolutionary experiment in whorl size increase which reaches its extreme in *G. vinitincta*.

Nautiliropa with pitted apical sculpture, depressed spire, and strong radial ribbing may be related to the *Gyrocochlea*–*Biomphalopa* complex even though radular morphology, penial structure, shell coiling pattern and microsculpture are against close relationship.

The highly modified *Letomola contortus* is possibly a derivative of the *Gyrocochlea*-level of specialisation which has undergone size and shell sculpture reduction associated with a shift in microhabitat to life on rock surfaces. Enlarged, bulbous protoconch and elongate genitalia indicate descent from a large ancestor whose organ systems are consistent with the elongate *Gyrocochlea* pattern. Barrier formation and sulcus development in *L. contortus* can be correlated with change to small size and altered lifestyle. The bilobed kidney (with acutely angled ureteric arms) is probably a secondary modification directly attributable to reduction in whorl count.

Rhophodon also has apertural lamellae but these are independently derived from those of *Letomola*. The coiling pattern, whorl profile and strong radial sculpture suggest affinities with *Gyrocochlea* lineage. However the apical sculpture does not.

Coenocharopa is diverse in subtropical rainforests. The various species lead relatively specialised lifestyles among the dirt particles of the litter, on rock surfaces, or among moss on logs. Their shells have undergone reduction in primary calcified sculpture and developed fine deciduous periostracal ribs and extensions. Radial apical sculpture, enlarged penial complexes and expanded epiphallic pore suggest distant relationship with the *Cralopa/Elsothera* complex.

Problems associated with *Discocharopa* have been discussed in the systematic section. In essence the subtropical *Discocharopa* may be a a locally derived group. Apical sculpture indicates possible relationships to the *Cralopa–Elsothera* group.

Egilomen is represented by the depressed, widely umbilicate and strongly ribbed *E. cochlidium* and the globose, almost imperforate, more heavily ribbed *E. globosa*. The bilobed kidney (without evidence of whorl number reduction) suggests a quite separate derivation to other radially-ribbed genera reviewed herein.

Omphaloropa varicosa with spirally lirate apex, wide umbilicus and large tubular penial verge does not appear to have any close equivalent among other subtropical species. Another species with spirally lirate protoconch, *Sinployea intensa*, represents a remnant of a more widespread Pacific group.

Epiphallic and penial modifications distinguish *Rotacharopa* while the peculiar apical sculpture relates the genus to the Pacific Island *Microcharopa* and North American *Radiodiscus*.

Knowledge of Australian Charopidae is still at a rudimentary level and reflected by the mosaic nature of morphological trends outlined above. Production of a formal generic phylogeny would be a futile exercise at this stage. Rather I have proposed a scheme of hypothesised relationships (Fig.149) which summarises the preceding discussion and information given elsewhere in this study. It identifies the probable multiple origins of the fauna and outlines major trends discussed herein.

PAUP

A preliminary computer-based cladistic analysis using PAUP was carried out. Seventy-five characters (42 anatomical, 33 conchological) (Appendix) were chosen and ordered. The resultant cladogram (Fig. 150) shows that taxa with highly differentiated shells such as *Coenocharopa* and *Omphaloropa* are distinguished from the more generalised groups such as *Gyrocochlea* and *Rhophodon*. However, there are also some unusual associations where a high degree of conchological convergence is involved, viz. *Ngairea levicostata* and *Mussonula verax* ; *N. murphyi* and *Hedleyoconcha delta*. *Egilomen globosa* is associated with the Rotadiscinae even though the latter has markedly different sculptural and anatomical features. *Elsothera* and *Cralopa* are associated with taxa lacking a complete secondary ureter and the conchologically specialised *Setomedea* is separated from other species lacking a complete secondary ureter. *Gyrocochlea*, *Biomphalopa* and *Nautiliropa* were grouped together, and the highly modified *Letomola contortus* was placed near these genera.

BIOGEOGRAPHY

The Australian charopid fauna possibly consists of 250–300 species but prior to the present study, which introduces 27 species, only 110 species level taxa had been named. Hence, with probably less than half the available species described, and an even smaller number subjected to detailed analysis, it is premature to be confident about understanding their biogeography. The treatment below provides a synoptic review of climatic, geologic and vegetational changes in the east coast region during the Tertiary; brief discussion of charopid distribution patterns; and synthesis placing the taxa of this study into broader biogeographic context.

BACKGROUND

In subtropical and tropical eastern Australia distribution of land snails and rainforest are linked. In the Charopidae, which is acknowledged to be a Gondwanan family (Van Bruggen, 1980), this relationship probably had its origins in the Late Cretaceous when mesic forests were more widely spread than at present. Since the Cretaceous few Charopidae have made the transition to drier sclerophyll forest, in spite of potent environmental change which has favoured the development of xerophilic communities. This indicates a strong ecological bond between these tiny snails and closed forests which is probably due to convergent habitat preference. The ecological factors which favour development and persistence of rainforests e.g. moisture and eutrophic soils, are also those which favour the success of terrestrial molluscs. For snails, rainforest also provides shelter and food. These conclusions are not very different from those of Solem, Climo and Roscoe (1981) who found that moisture and spatial quality were significant factors in the survival of snail species in the Manukau Peninsula area of New Zealand, and Boycott (1934), who considered that shelter, lime and moisture were key factors in determining local occurrences of British land molluscs.

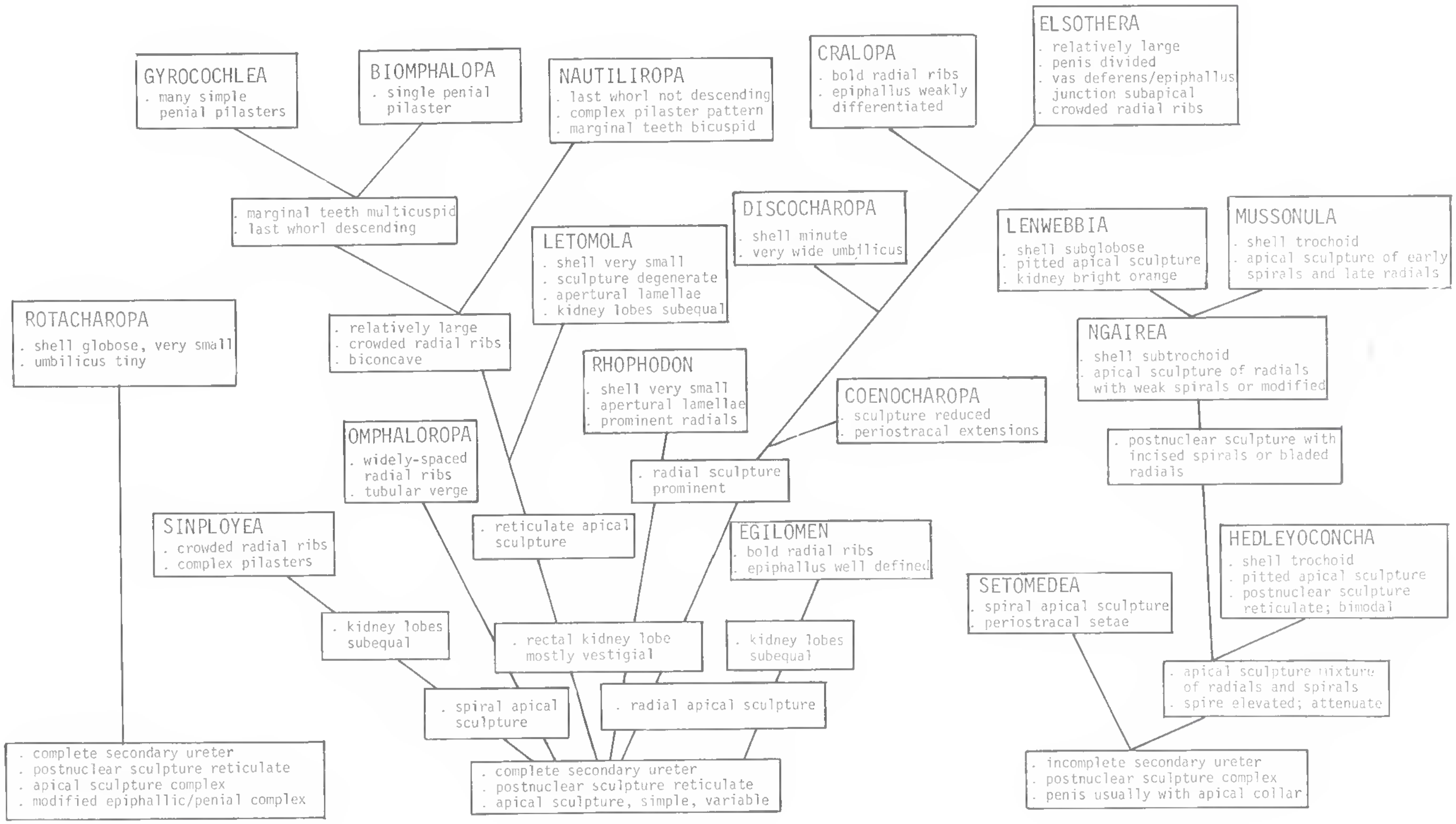
Australia separated from Gondwanaland in the early Tertiary reaching its present position at the edge of the Asian plate in the mid-Miocene (Kemp, 1981; Kemp and Galloway, 1981). In the early Tertiary, most of Australia would have resided within a weak band of wind circulation and the surrounding warm seas would have resulted in widespread precipitation. But with opening of the southern ocean and drift northward into lower latitudes, significant changes in climate occurred. Circum-polar circulation significantly reduced heat transport between the equator and pole resulting in latitudinal stratification of water temperatures. Consequently around the middle of the Miocene, the sea surface cooled and precipitation on land declined. From that time aridity has been a dominant factor in Australia's climate with wetter phases occurring only briefly. Rainforest communities, widespread at the beginning of the Tertiary, retreated to refugia and were replaced by a xeric adapted biota. However, in eastern Australia, two geological events contributed to the maintenance of mesic communities in the wake of the arid phases which elsewhere resulted in the removal of the widespread rainforest flora (Martin, 1978). Firstly, episodic uplift of the eastern highlands began in the Paleocene with major elevation occurring in the late Miocene and Pliocene. Secondly there was widespread igneous activity in eastern Australia along and adjacent to the eastern highlands (Wellman and MacDougall, 1974). In northern NSW vulcanism continued into the mid-Miocene while in SEQ peak activity occurred in the Oligocene and Plio-Pleistocene. The eastern highlands ensured orographic rainfall and enabled species to radiate altitudinally, while indirectly, vulcanism provided favourable soil-water conditions in a basically dry infertile continent. The fact that most land snails in eastern Australia now occur in 'rainforest' indicates that the persistence of moist refugia was critical to their survival in this region. The major refuges during these dry periods were in the moist uplands, and in lowlands along major drainage lines—areas which were not large, but wet.

Climatic changes in the late Quaternary were similar in amplitude to those experienced in the Miocene and Pliocene but occurred in more rapid succession. Galloway and Kemp (1981) concluded that these changes must have placed considerable stress on montane and coastal environments and that modern communities in these situations are recent phenomena consisting of biota which have survived in isolated refuges.

Recent studies by Kershaw (1980, 1981) on pollen samples from crater lakes on the Atherton Tableland, confirmed that the climatic fluctuations of the late Tertiary had dramatic effects on the Australian vegetation. Kershaw's results showed that between 83,500 and 79,000 BP, complex rainforest covered the Atherton Tableland under rainfall much higher than today. These conditions persisted until about 38,000 BP when a major change occurred and wet-adapted araucarian forests of the Atherton Tableland were replaced by drier communities characterised by *Eucalyptus* and *Casuarina*. These dominated the area until 8–10,000 BP when rainforest again emerged from retreats. Kershaw (1980, 1981) was further able to demonstrate that these local, environmental changes could be applied to other areas along the east coast.

The palynological studies of Kershaw (1981)

FIG. 149. Hypothesised relationships of charopid genera reviewed in this study


GYROCOCHLEA
. many simple penial pilasters
BIOMPHALOPA
. single penial pilaster
NAUTILIROPA
. last whorl not descending
. complex pilaster pattern
. marginal teeth bicuspid
CRALOPA
. bold radial ribs
. epiphallus weakly differentiated
ELSOTHERA
. relatively large
. penis divided
. vas deferens/epiphallus junction subapical
. crowded radial ribs
. marginal teeth multicuspid
. last whorl descending
DISCOCHAROPA
. shell minute
. very wide umbilicus
LETOMOLA
. shell very small
. sculpture degenerate
. apertural lamellae
. kidney lobes subequal
LENWEBBIA
. shell subglobose
. pitted apical sculpture
. kidney bright orange
MUSSONULA
. shell trochoid
. apical sculpture of early spirals and late radials
ROTACHAROPA
. shell globose, very small
. umbilicus tiny
. relatively large
. crowded radial ribs
. biconcave
NGAIREA
. shell subtrochoid
. apical sculpture of radials with weak spirals or modified
RHOPHODON
. shell very small
. apertural lamellae
. prominent radials
COENOCHAROPA
. sculpture reduced
. periostracal extensions
OMPHALOROPA
. widely-spaced radial ribs
. tubular verge
. postnuclear sculpture with incised spirals or bladed radials
. radial sculpture prominent
SINPLOYEA
. crowded radial ribs
. complex pilasters
. reticulate apical sculpture
EGILOMEN
. bold radial ribs
. epiphallus well defined
HEDLEYOCONCHA
. shell trochoid
. pitted apical sculpture
. postnuclear sculpture reticulate; bimodal
SETOMEDEA
. spiral apical sculpture
. periostracal setae
. kidney lobes subequal
. rectal kidney lobe mostly vestigial
. kidney lobes subequal
. apical sculpture mixture of radials and spirals
. spire elevated; attenuate
. spiral apical sculpture
. radial apical sculpture
. complete secondary ureter
. postnuclear sculpture reticulate
. apical sculpture complex
. modified epiphallic/penial complex
. complete secondary ureter
. postnuclear sculpture reticulate
. apical sculpture, simple, variable
. incomplete secondary ureter
. postnuclear sculpture complex
. penis usually with apical collar

and Martin (1981) demonstrated the drastic effects of mid to late Tertiary climate on mesic communities and exposed some important principles pertinent to east coast biogeography. Firstly, areas and their faunas have been isolated on a number of occasions thus promoting allopatric speciation, and subsequently unified to allow for dispersal and the evolution of sympatric congeneric pairs. Secondly, certain elements of the biota found in the "modern" northern Australia have been present in Australia for a long time and many of those taxa presently confined to the north were present in south-eastern Australia when it was adjacent to Antarctica. Thirdly, some species in northern Australia have become extinct in fairly recent times. These principles have particular application to a low vagility Gondwanan group of organisms such as the charopid land snails.

Webb (1959, 1968) expressed the results of past environmental changes through a present day classification of structurally based rainforest types. In a biogeographic synthesis, Webb and Tracey (1981) demonstrated that the popular concept of tropical and subtropical rainforest encompasses a complex mosaic of community types each reflecting a past series of climatic change. This division of the "rainforest massif" into regions and provinces associated with present climatic regimes, which at the same time reflected quite different histories of climatic change, provides a practical framework for interpreting the impact of these changes in the context of the fragmentation and isolation of mesic communities. At a regional level the results indicate that the cooler forests of the southeast (cool temperate to subtropical) have been separated from the warmer forests of the northeast (tropical), probably since the late Miocene aridity phases. A dry corridor between Gladstone and St Lawrence, geographically distinguished by a lack of coastal and subcoastal highlands, ensured that the biotas of the two regions developed in isolation while a dry corridor between Townsville and Bowen isolated the Eungella rainforests from the main massif of northern rainforest. At a provincial level, temperate forests of the cooler Tasmanian and Victorian regions are segregated from the more northern warm temperate, and cool to warm subtropical forest while a third drier subtropical forest type occurs subcoastally in southern Queensland.

Considering the close ecological ties between Charopidae and closed forests, Webb's rainforest classification makes it possible to relate past climatic and geological events to present day charopid distribution.

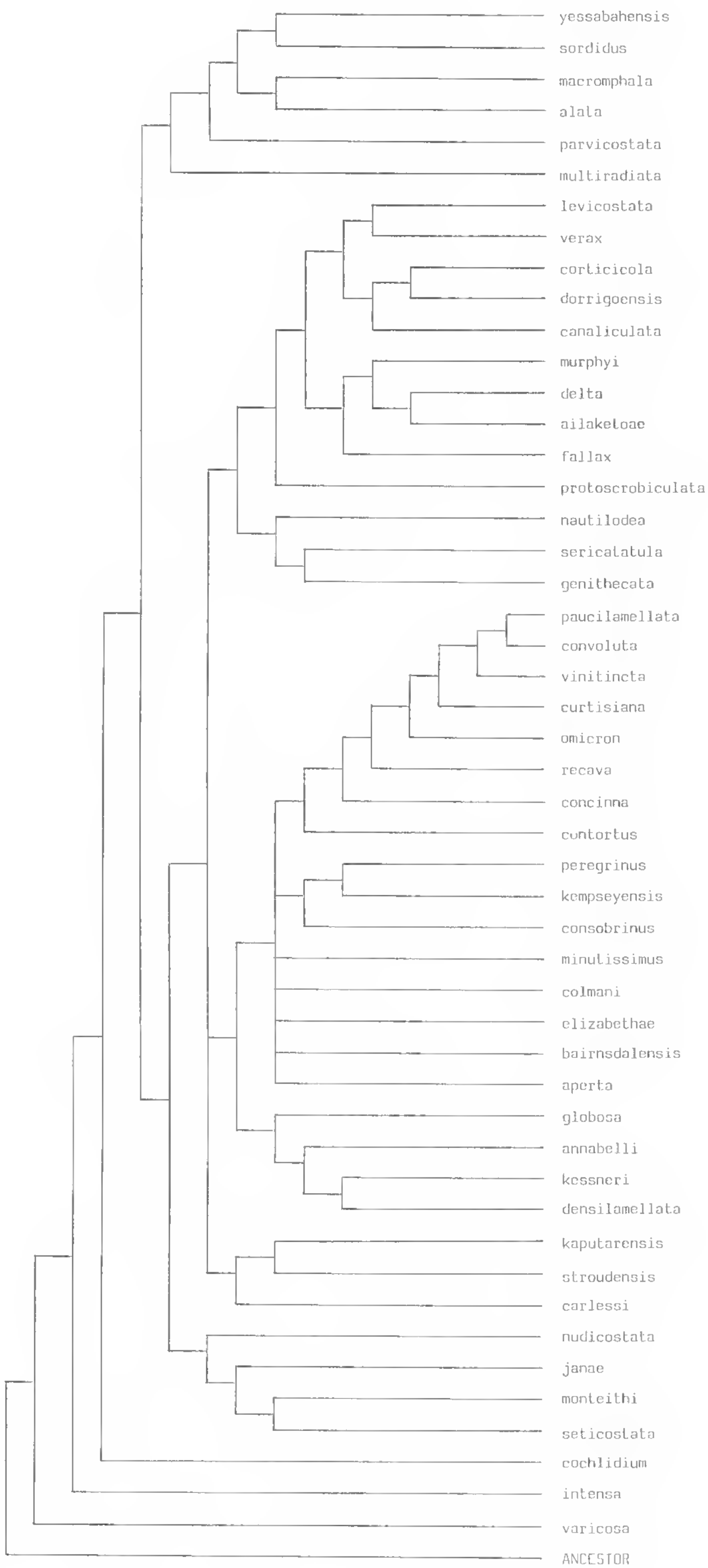
CHAROPID DISTRIBUTION

At the family level distribution of Charopidae in Australia is basically east coast. Species are found in moist cool temperate forest of the southeast region (Smith and Kershaw, 1979; Smith and Kershaw, 1985), warm temperate and subtropical forests of northern NSW and SEQ, in the structurally subtropical forests near Mackay, MEQ, and the tropical coastal forests between Ingham and Cooktown, NEQ. A small but significant radiation of charopids is also present in southwest Australia (Solem, 1983), several species exist across the north of the continent (Solem, 1984), and a presumably relict species '*Pillomena*' *aemula* (Tate, 1894), is found in the remnant mesophytic forest of Central Australia. All indications are that the distribution of the group in Australia was much more extensive in the past.

Of the 50 species reviewed herein 32 are endemic to the main area of subtropical rainforest between Dorrigo, NSW (30°30'S) and Rockhampton, MEQ (23°30'S). Three species viz. *Hedleyoconcha delta*, *Coenocharopa multiradiata* and *Cralopa stroudensis* extend further south, while 14 species occur outside this core region.

Discocharopa aperta from the drier rainforests of SEQ ranges to northern and central Australia, the Bismarcks, Philippines, Indonesia, New Hebrides, Kermadec, Fiji, Samoa, Austral and Society Islands (Solem, 1983, pp. 74–81). The small, semiarboreal *Sinployea intensa* has a long, narrow, coastal distribution which encompasses a number of sublittoral rainforest patches. Wide ranging species also include the litter dwelling *Omphaloropa varicosa* which is found from the McPherson Ranges on the NSW/Qld border, to west of Rockhampton, MEQ; *Setomedea seticostata* and *Ngairea dorrigoensis* which range from Dorrigo, NSW, to just north of Brisbane, SEQ; and the litter dwelling *Coenocharopa parvicostata* with a range from Dorrigo, NSW, to just north of Gympie, SEQ. The north-south linear ranges of these species are between 350–700 km and are the upper extremes where the majority of species have ranges of less than 200km. However in general the

FIG. 150. Consensus tree derived from PAUP analysis.


yessabahensis
sordidus
macromphala
alala
parvicostata
multiradiata
levicostata
verax
corticicola
dorrigoensis
canaliculata
murphyi
delta
ailaketoae
fallax
protoscrobiculata
nautilodea
sericatatula
genithecata
paucilamellata
convoluta
vinitincta
curtisiana
omicron
recava
concinna
contortus
peregrinus
kempseyensis
consobrinus
minutissimus
colmani
elizabethae
bairnsdalensis
aperta
globosa
annabelli
kessneri
densilamellata
kaputarensis
stroudensis
carlessi
nudicostata
janae
monteithi
seticostata
cochlidium
intensa
varicosa
ANCESTOR

ranges do not approach Solem's predicted value for all land snails of less than 50 km (Solem, 1984, p. 14).

With the exception of *Rhophodon colmani*, whose distribution is considered to be poorly known, the smallest linear ranges of subtropical endemic species are those of *Rhophodon elizabethae* and *Setomedea nudicostata* which occur in the relatively small and unusual moist subtropical refugium in the Bobby Range, southwest of Gladstone, SEQ. These examples suggest that species ranges may be determined by the size of particular rainforest patches and hence subject to considerable pressure from changing climatic conditions. *Coenocharopa yessabahensis*, *Rhophodon kempseyensis* and *Letomola contortus* from the Yessabah-Carrai limestone series, west of Kempsey, NSW, are further examples of environmentally restricted taxa.

Coenocharopa has four endemic, often overlapping species in subtropical forests with comparatively large linear ranges (180–486 km) indicating that the genus has undergone a long period of environmental sifting. In *Gyrocochlea*, linear ranges are relatively short (54–108 km) and patterns of overlap are minimal with only *Gyrocochlea vinitincta* and *G. paucilamellata* showing minor sympatric occurrence. It is probable that the *Gyrocochlea* radiation is a relatively recent phenomenon in the subtropical region.

Geographic distribution within a genus is generally north-south. *Rhophodon*, with a single species in the southeast region and six species from Kempsey, NSW, to the Bobby Range, SEQ, is illustrative. *Setomedea* and *Hedleyoconcha* have more striking disjunct north-south distributions with relict species in central and north Queensland. *Ngairea* has its main radiation in the subtropical forests but also has an outlier species in the Illawarra region of southern NSW. The southern limits of *Elsothera* are not known but its occurrence in the subtropical forest is also considered to be relict. As a rule, genera tend to have relicts in the north rather than vice versa indicating that some genera which are present in the south were also common in the north during cooler times.

A major exception to the typical north-south pattern is *Cralopa* which has a single widespread species, *C. stroudensis*, in the coastal and subcoastal subtropical rainforests; a closely related species, *C. kaputarensis*, on Mt Kaputar, west of Narrabri, NSW; and a further widespread, but geographically disjunct species, *C. carlessi*, on the limestone outcrops of the Great Dividing Range. Unlike other genera now confined to the east, *Cralopa* has been able to survive in largely snail depauperate areas further west.

Although patterns of geographic distribution are usually north-south, large wet areas such as the McPherson Ranges provide sufficient width in the rainforest massif to allow for localised speciation in an east-west direction, e.g. *Ngairea* and *Gyrocochlea*.

There is limited evidence for altitudinal differentiation. *Egilomen cochlidium* and *Coenocharopa alata* show preference for montane habitats in contrast to the foothill/lowland distribution of their congeners. *Ngairea corticicola* is microsympatric with *N. dorrigoensis* in the Great Dividing Range, and extends to the foothills whereas *N. dorrigoensis* occurs only in the highlands. Other examples are seen in *Gyrocochlea* and *Rhophodon*.

Coherent distribution patterns among closely related genera are less obvious but this is probably due to gaps in phyletic knowledge. Where patterns emerge they appear to be similar to those discussed above. *Gyrocochlea* which is an endemic subtropical group has its nearest relative, *Biomphalopa*, in the rainforests of central and north Queensland. In contrast the closely related *Mussonula*, *Lenwebbia* and *Ngairea* have overlapping distributions in SEQ.

PATHWAYS OF DIFFERENTIATION

I consider that the environmental changes associated with mid to late Tertiary aridity were the major factors affecting the present makeup and distribution of the Australian Charopidae. Two levels of changes are seen as particularly significant - those which produced generic differentiation and major intrageneric disjunctions, and those which produced fine grain distribution adjustments within larger areas of rainforest. The first level probably dates from the onset of aridity in the Miocene, while the second is most likely related to drastic short term climatic oscillations of the Quaternary.

In the north the formation of dry corridors between St Lawrence and Rockhampton, and Bowen and Townsville (Fig. 1) correlate with the current disjunct distributions of *Hedleyoconcha* and *Setomedea*. Persumably these groups once ranged along the entire moist coastal region from north Queensland to northern NSW. As mesic habitats retreated, the ancestral range became severely fragmented, and mid-east

Queensland and northeast Queensland populations would have been isolated from each other and from more southern subtropical rainforests. Arboreal *Hedleyoconcha* responded more dramatically disappearing from the notophyll vine forests of mid-east Queensland. In the north, *H. ailaketoae* survived only in the altitudinal refugia of Mt. Bellenden Ker, while in the south, persistence of suitable habitat enabled *H. delta* to flourish in a wide area of moist subtropical rainforest in northern New South Wales and southern Queensland.

Setomedea would have endured similar environmental pressures to *Hedleyoconcha* but, probably because of greater adaptability or peculiar microhabitat requirements, managed to maintain *S. janae* in mid-east Queensland, and at least two other species in north Queensland. In the north *Setomedea* was most likely restricted to montane refugia at some time in the drier past, but subsequently has been able to disperse into the foothills and lowlands (*S. monteithi*). In southern Queensland and northern New South Wales, *S. seticostata* (Hedley, 1924) occupies upland regufia as well as lowland notophyll vine forests also indicating dispersal from high to low altitudes in wetter times. Further examples of large-scale intrageneric disjunctions which can be related to mesic habitat regression include the separation of *Biomphalopa concinna* and *B. recava*, and the isolation of *Ngairea murphyi* in the Illawarra region, southern New South Wales, from the main mass of *Ngairea* species further north.

Creation of these major dry corridors probably also led to generic differentiation between north and south. This is best illustrated by the disjunct distribution of the closely related *Gyrocochlea* (southeast Queensland) and *Biomphalopa* (mid-east and north Queensland).

In southeast Queensland, regression of complex mesic habitats to upland refugia and their replacement by less complex microphyll vine forests in the lowlands between Gympie and Rockhampton, correlate with disjunctions in several groups. *Rhophodon elizabethae*, *Gyrocochlea curtisiana*, *Setomedea nudicostata* and *Ngairea canaliculata* occur within this region in wetter montane refugia and are geographically isolated from congeners further south. This isolation has been severe in *R. elizabethae* and *S. nudicostata* which are restricted to refugial notophyll vine forests in the Bobby Range, SW of Miriam Vale, and *N. canaliculata* which inhabits only the moist forests of the mountain summits between Colosseum Creek and Mt Larcom. In contrast *G. curtisiana* is found in both moist and dry forests. It probably survived climatic attrition in scattered refugia and subsequently dispersed into the drier microphyll vine forests and fringing open forest. In comparison with *R. elizabethae*, *S. nudicostata* and *N. canaliculata*, the larger *G. curtisiana* has less specific microhabitat requirements. It has more generalised pallial structures indicating that it may have had less difficulty in adapting to drier environments. The fragmented distribution of *Rotacharopa* is also probably due to these local environmental changes.

Although *Ngairea* has not colonised these drier microphyll vine forests, *Lenwebbia protoscrobiculata*, which is considered to be a derivative of the *Ngairea* group, has done so successfully.

Within the main humid subtropical rainforest block, which includes the Border Ranges, Great Dividing Range (from Dorrigo, NSW to the Mistake Mountains, SEQ) and their foothills and lowlands, charopid evolution has been much more complex. The long-term stability of these subtropical forests was ensured by the favourable volcanic soils and above average rainfall, even at lower altitudes. Hence while there was fragmentation and retreat of moist forest into favourable refugia such as gully heads, riverine alluvia and mountain summits in dry periods, alternate periods of higher rainfall would have led to many episodes of expansion and amalgamation. In some areas such as the drier western edges of the Border Ranges and Great Divide, and in places where soil types were poor, periods of lower rainfall did cause a shift in vegetation type to drier microphyll vine forest. In higher reaches e.g. Lamington Plateau, 'temperate' rainforest persisted in selected refugia. These events would have provided considerable opportunity for local speciation, dispersal and isolation. The results have been 'fine-grain' speciation patterns and evolution of several endemic genera.

The ancestral stock of *Gyrocochlea* presumably had a distribution which covered the uplands and lowlands of the eastern Border Ranges. Following climate-induced habitat fragmentation, the heavily ribbed *Gyrocochlea vinitincta* would have been isolated in higher parts of the Lamington Plateau from the sparsely ribbed forms of the foothills; and with the shift to drier forest types in western areas, *G. convoluta* became separated from more easterly *G. paucilamellata* which lives in the palm-dominated forests around the Darlington Range. In wetter times, *G. vinitincta* dispersed into the range of *G. paucilamellata*. Similarly evolution of local *Rhophodon* probably involved fragmentation of a wide ranging ancestral population into foothill (*R. consobrinus*) and upland (*R. peregrinus*) species. Subsequently *R. peregrinus* expanded its range to become sympatric with *R. consobrinus*.

Aridity episodes probably isolated the weakly ribbed *Ngairea corticicola* in the subtropical notophyll vine forests of the uplands and foothills from the heavily ribbed stock in more restricted temperate montane refugia. In the western highlands of the Border Ranges the development of drier vine forests effectively isolated *N. levicostata* from the widespread montane species, *N. dorrigoensis*. As aridity phases were replaced by periods of higher rainfall, *N. dorrigoensis* was able to disperse from montane refugia and gradually occupy the ranges of its two congeners.

It is more than coincidental that the expansion of rainforest during wetter periods favoured those species restricted to moist montane refugia. These communities were able to expand into lower areas where the soil type was suitable, and into areas with less suitable soils where rainfall was adequate. On the other hand the lowland and foothill rainforest communities isolated in gully heads would have expanded to produce a more contiguous block, but would not have expanded to higher altitudes. In contrast drier rainforests were environmentally cornered, and consequently, the charopids in them, limited in their dispersal e.g. *N. levicostata* and *G. convoluta*.

The ability to relate past events of climatic, geological and vegetational changes to present-day distribution patterns in the Charopidae varies from group to group. In *Coenocharopa*, which contains six species with widely differing microhabitat preferences, these events have produced a very complex pattern of species overlap. Indications are that the group has undergone a long period of environmental sifting that has blurred historical pathways. There is evidence for segregation of a mesic-adapted highland species (*C. alata*) and a species which became adapted to the more easterly warm moist notophyll vine forests of the foothills of the McPherson Ranges (*C. parvicostata*). In the north, *C. macromphala* and *C. sordidus* probably developed from a common ancestor in response to environmental change which isolated mesic communities in the D'Aguilar Range from the araucarian forests of the Blackbutt Range and Mt. Mudlo region. Most likely more than one instance of dispersal has brought about the complex sympatric patterns evident today.

Nautiliropa and *Mussonula* are endemic to this region and are probably recent local derivations of more generalised stock, viz. *Gyrocochlea* and *Ngairea* respectively.

Restriction of charopids to wetter coastal habitats during the latter half of the Tertiary did not necessarily mean complete extinction of the family from drier western, sclerophyll-dominated areas. Where conditions were favourable i.e. where moist refugia could exist, charopids persisted e.g. *Cralopa*. As mesic habitats retreated eastward in the face of increasing aridity, *C. kaputarensis* was isolated in the moist montane refugia of Mt Kaputar, near Narrabri, NSW, and a little further east, *C. carlessi* survived in scattered limestone refugia on the western edge of the Great Divide, albeit reduced to a series of cornered disjunct populations.

Limestone habitats are extremely important refuge zones for land snails. Along the Great Divide, they typically support remnants of once more prevalent wet-adapted vegetation. The rocks trap available moisture in crevices and also provide protection from wildfires thus enabling small island communities, quite different from those in the surrounding open forest, to be maintained. Land snails which inhabit these exceptional refugia benefit from an ample supply of calcium. Because of long term isolation and need to adapt to a lifestyle among and on rocks, endemicity and specialization among snails is usually high. Limestones of the Yessabah-Carrai block, west of Kempsey, are a case in point. Their isolation from the main subtropical rainforest block, presumably due to mesic habitat regression, has resulted in separation of several charopid species from northern congeners e.g. *Rhophodon kempseyensis* and *Coenocharopa yessabahensis*. The monotypic *Letomola*, which may be a derivative of the *Gyrocochlea* lineage of subtropical charopids, is also endemic to these limestones. All these species have highly differentiated shells and habitat-related radular modifications.

CONCLUSIONS

Origins of the eastern Australian subtropical charopid fauna appear to be diverse. Groups with primitive pallial configurations such as *Ngairea*, *Hedleyoconcha* and *Setomedea* are probably remnants of older stock with origins in the widespread Gondwanan biota. This group seems to have suffered extensively from mesic habitat regression although *Ngairea* has managed to secondarily diversify in the subtropical forests. *Mussonula* and *Lenwebbia* are most likely recent, local derivatives. *Cralopa* and *Elsothera* have shell and anatomical features relating them to New Zealand Charopidae and are probable descendants of southern based groups that have attenuated distributions in subtropical regions. *Coenocharopa* can be considered an early offshoot from this stem that radiated into diverse habitats in the subtropical region. *Rhophodon*, with widely separated species along the east coast is probably of southern origin representing an early attempt at habitat specialisation and like *Coenocharopa* and *Ngairea* has secondarily diversified in the subtropical forests. *Gyrocochlea*, *Biomphalopa*, *Nautiliropa* and *Letomola* are possibly part of the same lineage as *Rhophodon*, but more recent in origin. In the case of *Letomola* and *Nautiliropa* generic differentiation has been accompanied by dramatic changes in conchological and anatomical features.

Of other genera, *Sinployea* is a remnant of a larger Pacific Island radiation; *Egilomen* is of uncertain affinity but has anatomical features indicating only distant relationship with other subtropical groups; *Omphaloropa* has a conflicting combination of characters and unusual distribution pattern which suggest that its relationships may be with species well to the north or south; *Discocharopa* remains problematic; and *Rotacharopa* is related to Pacific Basin and north American species.

ACKNOWLEDGEMENTS

I owe special thanks to Mr Darryl Potter, Queensland Museum, for his assistance in many aspects of this project. I am most grateful to the late Dr Alan Solem, Field Museum of Natural History, Chicago, USA, for his critical comments and constant encouragement.

For the loan of material I thank staff of the Australian Museum, Sydney; Museum of Victoria, Melbourne; South Australian Museum, Adelaide; and British Museum of Natural History, London. Other material was generously provided by Graeme Annabell, Vince Kessner, and Terry Carless.

Numerous specimens used in this study were collected during field work funded by the Australian Biological Resources Survey (1981–83).

I wish to thank the following staff of the Queensland Museum - Dr Robert Raven (Arachnology) for his help with the SEM and computer analysis; Dr Geoff Monteith (Entomology) for providing material and important information on collecting sites; Ms Gudrun Sarnes (Technician, Queensland Museum) for help with the SEM; Mr Bruce Cowell and Mr Gary Cranitch (Photography) for their assistance with all aspects of photography. In the early stages of the project Miss Alison Green, formerly Technician, Queensland Museum assisted with SEM and field work.

For typing the manuscript, I am particularly grateful to Mrs Peta Woodgate, Queensland Museum.

This work is based on a thesis which was submitted in fulfilment of the requirements for the degree of Doctor of Philosophy at the University of Queensland (1988) and I would like to thank Professor Barrie Jamieson, Department of Zoology, for his guidance and criticisms.

Finally, I wish to thank a special friend, Jan, who has been most supportive during the course of this project.

LITERATURE CITED

ANCEY, C.F. 1888. Nouvelles contributions malacologiques. *Bull. Soc. Malac. France*, 5: 341–376.

BAKER, H.B. 1927. Minute Mexican land snails. *Proc. Acad. Nat. Sci. Phila.*, 79: 223–246, pls. 15–20.

BAUR, G.N. 1959. Nature and distribution of rainforests in New South Wales. *Aust. J. Bot.*, 5: 190–233.

BISHOP, M.J. 1981. The biogeography and evolution of Australian land snails. In: A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 924–954. W. Junk Publ. The Hague, Netherlands.

BOYCOTT, A.E. 1934. The habitats of land Mollusca in Britain. *J. Ecol.*, 22: 1–38.

BROADBENT, J. AND CLARK, S. (eds). 1976. *A faunal survey of east Australian rainforests*. Australian Museum, Sydney.

BURCH, J.B. 1976. Outline of classifications of Australian terrestrial molluscs (native and introduced). *J. Malac. Soc. Aust.* 3: 127–156.

CLIMO, F.M. 1969a. Classification of New Zealand Arionacea (Mollusca: Pulmonata). I. The higher classification. *Rec. Dominion Mus. Wellington*, 6(12) : 145–158, 5 figs.

1969b. Classification of New Zealand Arionacea (Mollusca: Pulmonata). II. A revision of *Charopa* Subgenus *Ptychodon* Ancey, 1888. *Rec. Dominion Mus. Wellington*, **6**(14) : 175–258, 34 figs., pls. 1–11.

1970. Classification of New Zealand Arionacea (Mollusca: Pulmonata). III. A Revision of the genera *Charopa* Albers, 1860 (excluding subgenus *Ptychodon* Ancey, 1888), *Phenacharopa* Pilsbry, 1893, and *Flammocharopa* n. gen. (Endodontidae: Endodontinae). *Rec. Dominion Mus. Wellington*, **6**(18) : 285–366, 22 figs., pls. 1–9.

1971a. Classification of New Zealand Arionacea (Mollusca: Pulmonata). IV. A revision of the subfamily Otoconchinae Cockerell (Punctidae Morse). *Rec. Dominion Mus. Wellington*, **7**(6) : 43–49, 2 figs.

1978. Classification of New Zealand Arionacea (Mollusca: Pulmonata). A review of the New Zealand charopine snails with lamellate apertures. *Rec. National Mus. N.Z.*, **1**(12): 177–201.

1980. Classification of New Zealand Arionacea (Mollusca : Pulmonata). VII. The genera *Aeschrodomus* Pilsbry and *Pulchridomus* n.gen. (Charopidae). *Rec. National Mus. N.Z.*, **1**(18): 293–303, figs 1–5.

1981. Classification of the New Zealand Arionacea (Mollusca : *Pulmonata*). VIII. Notes on some charopid species, with description of new taxa (Charopidae). *Rec. National Mus. N.Z.*, **2**(3): 9–15, figs. 1–2.

1983. Classification of the New Zealand Arionacea (Mollusca : Pulmonata). IX. The new genus *Paracharopa* (Charopidae). *Rec. National Mus. N.Z.*, **2**(14): 151–161, figs 1–6.

1984. Classification of the New Zealand Arionacea (Mollusca : Pulmonata). X. *Montaropa macsweeneyi* n.gen., n.sp. (Charopidae) and the identity of *Flammulina alpina* Suter, 1904. *Rec. National Mus. N.Z.*, **2**(19): 207–210, fig. 1.

COTTON, B.C. 1939. Mollusca. In: The Sir Joseph Banks Islands. Reports on the expedition of the McCoy Society for Field Investigation and Research. *Proc. R. Soc. Vict.*, **51**(1): 159–176, pl. 7.

COX, J.C. 1864. *Catalogue of specimens of Australian land shells in the collections of J.C. Cox*. J.A. Engel, Sydney, Aust.

1866a. Description d'especes nouvelles provenant d'Australie et des iles Solomon et Norfolk. *Journ. de Conchyl.*, **14**: 45–48.

1866b. Characters of six new Australian land-shells. *Proc. Zool. Soc. Lond.*, 1866, pp. 373–375.

1868. *A monograph of Australian land shells*. 110 pp. + 22 pls. W. Maddock, Sydney.

1909. *An alphabetical list of Australian land shells*. Part I, 84 pp. and corrections. F.W. White, Sydney.

COX, J.C. and Hedley, C. 1912. An index to the land shells of Victoria. *Mem. Nat. Mus. Melb.*, **4**: 5–15, pls 1–3.

CUMBER, R.A. 1961. A revision of the genus *Phenacohelix* Suter, 1892 (Mollusca : Flammulinidae) with description of new species, and studies on variation, distribution and ecology. *Trans. R. Soc. N.Z.*, **1**(13): 163–196.

GABRIEL, C.J. 1930. Catalogue of the land shells of Victoria. *Proc. Roy. Soc. Vict.*, **43**(1): 62–88, pls. 2–3.

1947. Additions to and alterations in the catalogue of the land shells of Victoria (including descriptions of new species). *Mem. Nat. Mus. Vic.*, **15**: 109–125, pls 9–10.

GABRIEL, C.J. and Macpherson, J.H. 1947. Mollusca. In: A preliminary report on the biology and ecology of the Snowy River area in northeastern Victoria. *Mem. Nat. Mus. Vic.*, **15**: 146–171, pls 11–13.

GALLOWAY, R.W. AND KEMP, E.M. 1981. Late Cainozoic environments in Australia. In: A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 52–80. W. Junk Publ., The Hague, Netherlands.

HEDLEY, C. 1889. Anatomical notes on the Helicidae, Part III. *Proc. Roy. Soc. Queensland*, **6**: 249–251, pls 14–15.

1892. Observations on the Charopidae. Part I. *Proc. Linn. Soc. NSW*, **7**: 157–169, pls 1–2.

1899. Descriptions of new land shells with notes on known species. *Rec. Aust. Mus.*, **3**: 151–154, pl. 28.

1912. On some land shells collected in Queensland by Mr Sidney W. Jackson. *Proc. Linn. Soc. NSW.*, **37**: 253–270, pls 4–10.

1924. Some notes on Australian land shells. *Aust. Zool.*, **3**: 215–222, pls 29–32.

HEDLEY, C. AND MUSSON, C.T. 1892. On a collection of land and freshwater shells from Queensland. *Proc. Linn. Soc. N.S.W.*, **6**(3): 551–564.

IREDALE, T. 1933. Systematic notes on Australian land shells. *Rec. Aust. Mus.*, **19**: 37–59.

1937a. A basic list of the land Mollusca of Australia. *Aust. Zool.*, **8**(4): 287–333.

1937b. A basic list of the land Mollusca of Australia. Part II. *Aust. Zool.*, **9**(1): 1–39, pls 1–3.

1937c. An annotated checklist of the land shells of south and central Australia. *S. Aust. Nat.*, 18: 6–56, pls 1–2.

1939. A review of the land Mollusca of Western Australia. *J. Roy. Soc. West. Aust.*, 25: 1–88, pls 1–5.

1941a. Guide to the land shells of New South Wales. Part II. *Aust. Nat.*, 10(8): pp. 262–269, figs. 4–6.

1941b. Guide to the land shells of New South Wales. Part III. *Aust. Nat.*, 11(1): pp. 1–8, figs. 7–8.

1942. Guide to the land shells of New South Wales. Part IV. *Aust. Nat.*, 11: 33–40.

1944. The land Mollusca of Lord Howe Island *Aust. Zool.*, 10(3): 299–334, pls 17–20.

KEMP, E.M. 1981. Tertiary palaeogeography and the evolution of Australian climate. In: A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 32–49. W. Junk Publ. The Hague, Netherlands.

KERSHAW, A.P. 1980. Long term changes in north-east Queensland rainforest. In: J. Wright, N. Mitchell, P. Watling (Eds), *Reef, Rainforest, Mangroves, Man*, pp. 32–38. Wildlife Preservation Society of Queensland publ., Brisbane, Aust.

1981. Quaternary vegetation and environments. In: A. Keast (ed.), *Ecological Biogeography of Australia*. pp. 81–101. W. Junk Publ. The Hague, Netherlands.

KERSHAW, R.C. 1954. Studies on Australian Charopidae (Mollusca, Pulmonata) Part 1 - The shell, its distribution and habitation. *Vic. Nat.*, 71: 95–96.

1955. Studies on Australian Charopidae. Part 2 - Some genera. *Vic. Nat.*, 72: 28–30.

1956a. Studies on Australian Charopidae. Part 3 - Planate genera. *Vic. Nat.*, 72: 137–143.

1956b. Studies on Australian Charopidae. Part 4 - Convex genera. *Vic. Nat.*, 73: 7–9.

MARTIN, H.A. 1978. Evolution of the Australian flora and vegetation through the Tertiary: evidence from pollen. *Alcheringa*, 2: 181–202.

MARTIN, H.A. 1981. The Tertiary flora. In: A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 391–406. W. Junk Publ., The Hague, Netherlands.

MONTEITH, G.B. 1980. Relationships of the genera of Chinamyersiinae, with description of a relict species from mountains of North Queensland (Hemiptera : Heteroptera : Aradidae). *Pacific Insects*, 21(4): 275–285.

ODHNER, N.H. 1917. Mollusca. XVII. Results of Dr E. Mjobergs Swedish Scientific Expedition to Australia 1910–1913. *Kungl. Svenska. Vetenskap Handl.*, 52(16): 1–115.

PETTERD, W.F. and Hedley, C. 1909. A revised census of the terrestrial Mollusca of Tasmania. *Rec. Aust. Mus.*, 7: 283–304, pls 82–87.

PFEIFFER, L. 1850. Descriptions of twenty-four new species of Helicea from the collection of Hugh Cuming, Esq. *Proc. Zool. Soc. Lond.*, 1849, pp. 126–131.

1851. Neue Molluskengattungen. *Zeitschr. fur Malak.*, 8: 126–131.

1854. Die Helicacea. In: Martini and Chemnitz (Eds). *Systematisches Conchylien Cabinet*, Bd I. Ab. 12(2): 1–562, pls 67–167.

1857. Descriptions of thirty-three new species of land shells from the collection of H. Cuming, Esq. *Proc. Zool. Soc. Lond.*, 1856, pp. 385–392.

PILSBRY, H.A. 1893. *Manual of Conchology*, 2nd series. 9: 1–366, pls 1–71, plus index 126 pp.

REEVE, L. 1851–57. *Conchologia Iconica or illustrations of the shells of molluscous animals*. Vol. 7, parts 1 and 2, species 1–1495.

SHIRLEY, J. 1921. Land shells of the Queensland National Park. *Qld. Nat.*, 3(2): 32–37.

SINGH, G. 1982 Environmental upheaval: vegetation of Australasia during the Quaternary In: J.M.B. Smith (ed.), *A History of Australasian Vegetation*, pp. 90–108, McGraw-Hill, Sydney, Aust.

SMITH, B.J. AND KERSHAW, R.C. 1979. *Field guide to the non-marine molluscs of South Eastern Australia*, 285 pp. ANU Press, Canberra.

1981. *Tasmanian land and freshwater molluscs*. Fauna of Tasmania Handbook, 5. pp.1–148. Hobart, Tasmania.

1985. Description of three Tasmanian charopid genera (Pulmonata : Mollusca) with notes on their type species. *Rec. Queen Victoria Mus. Launceston*, 88: 1–14, pls 1–5.

SOLEM, A. 1970. The endodontid land snail genera *Pilsbrycharopa* and *Paryphantopsis* (Mollusca; Pulmonata). *Veliger*, 12(3): 239–264.

1972. Malacological applications of scanning electron microscopy. II. Radular structure and functioning. *Veliger*, 14(4): 327–336, 4 pls.

1973. Apertural barriers in Pacific Island land snails of the families Endodontidae and Charopidae. *Veliger*, 15(4): 300–306, 24 figs.

1976. Endodontoid land snails from Pacific Islands. Part 1. Family Endodontidae. *Fieldiana: Zool. Spec. Publ.*, pp. 1–508, 208 figs.

1977. Shell microsculpture in *Striatura*, *Punctum*, *Radiodiscus* and *Planogyra* (Pulmonata). *The Nautilus*, 91(4): 149–155, figs 1–18.

1978. Classification of the land Mollusca. In: V. Fretter and J. Peake (Eds). *Pulmonates Vol. 2A*,

pp. 49–97.Academic Press, London and New York.
1983. Endodontoid land snails from Pacific Islands (Mollusca : Pulmonata : Sigmurethra). Part II. Families Punctidae and Charopidae, Zoogeography. *Field Museum of Natural History*, Chicago, 336 pp.
1984. Small land snails from northern Australia, III : Species of Helicodiscidae and Charopidae. *J. Malac. Soc. Aust.*, **6**(3/4): 155–179, figs 1–45.

SOLEM, A. AND CLIMO, F.M. 1985. Structure and habitat correlations of sympatric New Zealand land snail species. *Malacologia*, **26**(1–2): 1–30.

SOLEM, A., CLIMO, F.M. AND ROSCOE, D.J. 1981. Sympatric species diversity of New Zealand land snails. *N.Z. Journ. Zool.*, **8**: 453–485.

STANISIC, J. 1987. Studies on the Charopidae of tropical and subtropical Australia. I. *Oreokera*: a primitive genus from the high mountains of North Queensland (Mollusca : Pulmonata : Charopidae). *J. Malac. Soc. Aust.*, **8**: 1–21, figs 1–5, pls 1–2.
1988. A reevaluation of the relationships of *Helix (Thalassia) gayndahensis* Brazier, 1875 (Mollusca : Pulmonata : Helicarionidae). *Mem. Qd Mus.*, **25**(2): 475–479.

TRYON, G.W. 1885. *Manual of Conchology*, 2nd series, **1**: 1–364, pls. 1–60.
1886. *Manual of Conchology*, 2nd series, **2**: 1–265, pls. 1–64.
1887. *Manual of Conchology*, 2nd series, **3**: 1–313, pls. 1–63.

VAN BRUGGEN, A.C. 1980. Gondwanaland connections in the terrestrial molluscs of Africa and Australia. *J. Malac. Soc. Aust.*, **4**(4): 215–222, figs 1–4.

VAN DYCK, S. 1982. The status and relationships of the Atherton antechinus, *Antechinus godmani* (Marsupialia : Dasyuridae). *Aust. Mammal*, **5**: 195–210.

WEBB, L.J. 1959. A physiognomic classification of Australian rain forests. *J. Ecol.*, **47**: 551–570.
1968. Environmental relationships of the structural types of Australian rainforest vegetation. *Ecology*, **49**(2): 296–311.

WEBB, L.J. AND TRACEY, J.G. 1981. Rainforests: patterns and change. In: A. Keast (ed.), *Ecological Biogeography of Australia*, pp. 606–694. W. Junk Publ., The Hague, the Netherlands.

WELLMAN, P. AND MACDOUGALL, I. 1974. Cainozoic igneous activity in eastern Austraila. *Tectonophysics*, **23**: 49–65.

APPENDIX

LIST OF CHARACTERS AND CHARACTER STATES USED IN PAUP ANALYSIS

1.Tail differentiation (absent,0; present,1)
2.Foot shape (short broad, 0; bluntly rounded,1; slender tapered,2)
3.Kidney shape (bilobed,0; moderately bilobed,1; weakly bilobed,2; almost unilobed,3)
4.Configuration of kidney apex (simple,0; reflexed,1)
5.Primary ureter configuration (simple,0; reflexed,1; coiled,2)
6.Length of secondary ureter (incomplete,0; complete,1)
7.Number of lobes in ovotestis (one,0; two,1; several,2)
8.Ovotestis orientation (parallel,0; right angles,1)
9.Ovotestis shape (palmately clavate,0; finger-like,1; bilobed,2; unilobed,3)
10.Length of talon stalk (long,0; medium,1; very short,2)
11.Talon shape (circular,0; finger-like,1)
12.Hermaphroditic duct kinking (unikinked,0; kinked,1)
13.Vas deferens shape (thin,0; weakly expanded,1; strongly expanded,2)
14.Nature of epiphallus - vas deferens junction (simple,0; complex,1)
15.Differentiation of epiphallus (strong,0; weak,1)
16.Presence of epiphallus (present,0; absent,1)
17.Presence of epiphallic sheath (absent,0; present,1)
18.Epiphallus length (short,0; elongate,1)
19.Epiphallic pilaster pattern (longitudinal,0; transverse,1)
20.Epiphallus configuration (ascending arm longer,0; ascending/descending arms equal,1)
21.Nature of epiphallus - penis junction (simple,0; complex,1)
22.Position of epiphallus - penis junction (apical,0; subapical,1)
23.Nature of epiphallic entry into penis (through pore,0; through verge,1)
24.Position of penial retractor muscle insertion (penis,0; penis/epiphallus junction,1; epiphallus near penis,2; epiphallus far from penis,3)
25.Presence of epiphallus - penis binding (absent,0; present,1)
26.Presence of penis sheath (absent,0; present,1)
27.Penis shape (pear shaped,1; tubular,1)
28.Penis expansion (slender,0; moderately expanded,1; strongly expanded,2)
29.Presence of penial verge (absent,0; present,1)
30.Penial pilaster pattern (longitudinal,0; modified,1)

31.Presence of internal penial collar (absent,0, present,1)
32.Shape of genitalia (expanded,0; elongate,1)
33.Length of atrium (short,0; moderately long,1; very long,2)
34.Length of vagina (short,0; moderately long,1; very long,2)
35.Presence of preputial tube (absent,0; present,1)
36.Presence of penial stimulatory pad (absent,0; present,1)
37.Presence of flared extension on radular teeth (absent,0; present,1)
38.Configuration of radular row (transverse,0; v-shaped,1)
39.Nature of central tooth (strongly tricuspid,0; weakly tricuspid,1)
40.Nature of lateral teeth (tricuspid,0; bicuspid,1)
41.Presence of lateromarginals (present,0; absent,1)
42.Nature of marginal teeth (multicuspid with variable-sized cusps,0; other,1)
43.Shell coiling pattern (loose,0; normal,1; tight,2)
44.Nature of sutures (impressed,0; strongly impressed,1; channelled,2)
45.Presence of apertural barriers (absent,0; present,1)
46.Presence of supraperipheral sulcus (absent,0; present,1)
47.Shape of umbilicus (closed,0; narrow-u,1; narrow-v,2; wide-v,3; cup-shaped,4; saucer shaped,5)
48.Whorl profile (keeled,0; angulate,1; flattened above and below,2; rounded,2; rounded below,4; laterally compressed,5)
49.Number of whorls (3.0–3.5,0; 3.5–4.0,1; 4.0–4.5,2; 4.5–5.0,3; 5.0–5.5,4; 5.5–6.0,5; 6.0–6.5,6)
50.Height of shell (0–1 mm,0; 1–2 mm,1; 2–3 mm,2; 3–4 mm,3; 4–5 mm,4; 5–6 mm,5; 6–7 mm,6)
51.Shell diameter (1–2 mm,0; 2–3 mm,1; 3–4 mm,2; 4–5 mm,3; 5–6 mm,4; 6–7 mm,5; 7–8 mm,6)
52.H/D ratio (0.40–0.50,0; 0.51–0.60,1; 0.61–0.70,2; 0.71–0.80,3; 0.81–0.90,4)
53.Spire protrusion (depressed,0; 0.01–0.20 mm,1; 0.21–0.50 mm,2; 0.50–1.00 mm,3; 1.00–2.00 mm,4)
54.Body whorl width (0.01–0.50 mm,0; 0.51–1.00 mm,1; 1.01–1.50 mm,2; 1.51–2.00 mm,3; 2.01–2.50 mm,4; 2.51–3.00 mm,5; 3.01–3.50,6)
55.SP/BWW ratio (0.00–0.10,0; 0.11–0.20,1; 0.21–0.30,2; 0.31–0.40,3; 0.41–0.50,4, 0.51–0.60,5; 0.61–0.70,6)
56.Number of ribs on body whorl (25–50,0; 51–75,1; 76–100,2; 101–125,3; 126–150,4; 151–175,5; 175–,6)
57.Ribs/mm (0.01–5.00,0; 5.01–10.00,1; 10.01–15.00,2; 15.01–20.00,3; 20.01–25.00,4; 25.01–30.00,5; 30.01–35.00,6)
58.Umbilical width (closed,0; 0.01–0.50,1; 0.51–1.00,2; 1.01–1.50,3; 1.51–2.00,4)
59.D/U ratio (0.01–2.50,0; 2.51–5.00,1; 5.51–7.50,2; 7.51–10.00,3; 10.00–closed,4)
60.Nature of apical sculpture (spiral,0; predominantly radial,1; other,2)
61.Presence of radials on terminal part of protoconch (absent,0; present,1)
62.Presence of regular pits on protoconch (present,0; absent,1)
63.Presence of irregular pits on protoconch (present,0; absent,1)
64.Presence of apical spiral grooves (present,0; absent,1)
65.Presence of apical spiral segments (present,0; absent,1)
66.Presence of post nuclear spiral grooves (present,0; absent,1)
67.Presence of post nuclear spiral furrows (present,0; absent,1)
68.Presence of two–part sculpture on adult whorls (present,0; absent,1)
69.Presence of post nuclear microradials (present,0; absent,1)
70.Presence of periostracal blades on major ribs (present,0; absent,1)
71.Presence of post nuclear periostracal setae (present,0; absent,1)
72.Shell colour (monochrome,0; flammulated,1)
73.Presence of large major radial ribs (present,0; absent,1)
74.Presence of 'elongate-bead' microsculpture (present,0; absent,1)
75.Nature of beaded microsculpture (elongate,0; circular,1)

DATA FOR PAUP ANALYSIS

1.Option Settings

NOTU	50
NCHAR	75
User-tree(s)	NO
HYPANC	50
ADDSEQ	CLOSEST
HOLD	1
SWAP	GLOBAL
MULPARS	YES
OPT	FARRIS
ROOT	ANCESTOR
Weights applied	NO
OUTWIDTH	80
Missing data code	9
MAXTREE	100

2.Statistics Derived from Consensus Tree

Consensus fork index (component count) = 42
CF (normalised) = 0.875
Term information = 400
Mickevich's consensus information (CI) - 0.290
Levels sum - 6473
Rohlf's CI(1) = 0.813
Rohlf's - log CI(2) = 0.16566E+.03
Weighted consensus fork = 0.361

PAUP DATA MATRIX

Character states for species in order of listing above.

```
dorrigo:
  002000110??10000000000020001001000001011001000213351343??14101111111011111?
levicos:
  002000??????????????????????????????1001001000212443343??14201011011101011?
murphyi:
  003000210110000001000100000100110200100100200020434133 4??31101111111101011?
cortici:
  00200011010100000000000200010010000010110010002133513 43??23201101011101111?
canalic:
  002010110?00000001000011000100100000101100130022335134 2??23201101011101111?
protosc:
  0020102201000000000000001000100000000000101100242232241??22201011010011011?
delta:
  1020002201110000000000000001001122001000101000206663456??23201011110111011?
ailaket:
  102000220111000000000001000100110200100010100020445344 6??23201011110111011?
seticos:
  002120200200000000011020001000001010000000110034322122111310011111010101 01?
nudicos:
  002120200200000000000300011000010000000002100231111212221210011111110111 01?
janae:
  002120200200000000010020001000001000000000110034312112111310011111010101 01?
monteit:
  002120200200000000010000010100010000000000110034423223210310011111010101 01?
verax:
  ??????????????????????????????????????????10002114443353114211111011111011?
fallax:
  002010??????????????????????????????1001001000212342334??22211111111111011?
intensa:
  020001000200000000000?0000101?0010?000000110033111011122210011111110110000
varicos:
  010001100000000000000010010100001100000000110044211111200200011111110011001
vinitin:
  022001110101100001000110111000012200000000110043246106030411011111110110 01?
convolu:
  022001100??01000010001001110000122000000001100453341050104110111111101100 1?
paucila:
  022001100000100001000100111000012200000000110045234204000411011111110110 01?
curtisi:
  022001100000100001000100111000012200000000110043224114031412001111110111 01?
recava:
  022001100100000000000100001010012200000000210045423103021402001111110111 01?
concinn:
  022001100100000000000100001000012200000000210045312102021312001111110110 01?
omicron:
  022001100000000000000000000100001101011011111003322410403131200111110011 01?
contort:
  010001001200000000000001001000011201001001211 15?1010010??21201011111011011?
cochlid:
  010001100200000000000002000100000101000000012003431111110121101111110110001
globosa:
  010001100100000000000003000100012201000000210003311321411041011111110110001
stroude:
  011101100100201000000000001200000100000000120023211111122131011111110110 01?
kaputar:
  011101100000201000000002001200000100000000120003200111112041011111101100 1?
carless:
  011101100110201000000000001200002100000000120023212121311221011111101100 1?
peregri:
  012101100100000000000001010100012201000000211054300001055201011111110111000
consobr:
  012101100100000000000101010101010001000000211054301011044211011111110111000
```

```
kempsey:
  0121011001000000010000010101000122000000000211054411001066301011111110111000
minutis:
  0121011001000000000000001000100010200000000211054300011023201011111110110000
colmani:
  ??????????????????????????????????????????2110542000101012010111111110110000
elizabe:
  0121011001000000000000001000100012200000000211054311011111301011111110111000
bairnsd:
  0121011010000000000000001000100011200000000211054301011001201011111110110000
nautilo:
  ??????????????????????????????????????????110023223113052131011111111011001?
sericat:
  0221011001000100000000001000100100200000000110003223123152041011111111011001?
genithe:
  022101100110010011000003000100100200000000020103224103041041011111111011001?
sordidu:
  01200110010020000100000101010100200000000001100322221222??31101111111001011?
macromp:
  01200110020000000000000111010000110000000011003221112120021101111111001011?
parvico:
  01????100?00000000000000200010000010000000011003221111112??21101111111001011?
alata:
  012001100??00000000000000211010000220000000011003511112 13??21101111111001011?
multira:
  ??????????????????????????????????????????110033111111101211011111111001011?
yessaba:
  0120011001000000000000002010101000101000000110025212122 1??21101111111001011?
annabel:
  022001102?0000000001100040001010101100000002100135112111011220111011100100000
kessner:
  02200110210000000001100030001100102100000002100134112111221320111011100100000
densila:
  02200110200000000001100030001000102100000002100134103213441120111011100100000
aperta:
  022121101110 0??1?????????00100?02200??????10005300001012610101111111110110000
```